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14. ABSTRACT The proposed work has two objectives to improve prediction and assessment capabilities. The first objective is to determine if the generalized equation provided by our new gait mechanics model predicts the metabolic cost of weighted and unweighted walking more accurately than existing generalized equations. Our second objective is to determine how accurately weighted and unweighted walking metabolic rates can be estimated in field settings from simple technologies. Metabolic rates will be measured from expired gases. The timing of each walking stride, as well as its subcomponents (i.e. the contact and leg swing portions) will be determined from video. In addition, the periods of muscular activity responsible for executing the movements of the walking stride will be also assessed from electrical activity using surface electrodes attached to the skin above target muscles. The forces that subjects apply to the ground during locomotion may be measured from either a force plate or force sensors built into a treadmill. Finally, heart rate monitors to measure heart beat frequency, miniature motion sensors mounted to the shoe or other parts of the body to measure movement speeds and rates may also be utilized.					
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INTRODUCTION

The proposed work has two objectives coordinated to fulfill the overall objective of improving quantitative estimates of locomotor metabolism and activity in field settings. The objective of the first portion of the experimental work is to develop generalized equations that relate height, weight and speed to the metabolic rates incurred during walking. Fulfilling this objective will involve assessing whether the generalized equations provided by our new gait mechanics model will predict the metabolic cost of weighted and unweighted walking more accurately than existing generalized equations under controlled conditions. Our second objective is to determine how accurately weighted and unweighted walking metabolic rates can be estimated in field settings using simple, inexpensive wearable technologies.

Metabolic rates will be measured from expired gases. The timing of each walking stride, as well as its subcomponents (i.e. the contact and leg swing portions) will be determined from video and/or ground reaction force data. In addition, the periods of muscular activity responsible for executing the movements of the walking stride may be assessed from electrical activity using surface electrodes attached to the skin above target muscles. The forces that subjects apply to the ground during locomotion may be measured from either a force plate or force sensors built into a treadmill. Finally, miniature motion sensors and geolocation devices mounted to the shoe or other parts of the body to measure movement speeds and rates will also be utilized.

Field trials will be conducted using lightweight, portable indirect calorimeters. Subjects will walk both with and without weighted backpacks during both the laboratory and field trials.

BODY:

The total number of subjects tested during the project period was sixty-four. Per the statement of work, the project has focused on model testing and development for the following objectives: 1) to use our walking metabolism model to develop a generalized equation provided to predict the metabolic cost of walking more accurately than existing generalized equations, 2) to estimate how accurately weighted walking metabolic rates can be estimated in field settings from simple technologies, and 3) to use our walking metabolism model in conjunction with heart rate data to attempt to develop a walking test of aerobic fitness.

Thirty-six of the subjects tested completed resting metabolic rate tests, walking metabolism tests and maximal aerobic metabolism tests. The experimental; progression has revealed

that quantifying resting metabolic rate is an important for accurate interpretation and understanding of walking metabolism.

This recognition, made possible by the award, led to the literature test of our walking metabolism (also Height-Weight-Speed) model detailed below. Accurate quantification of the influence of walking metabolism is also essential for accurately quantifying the influence of loading on walking metabolic rates. The understanding of loaded walking remains in progress and cannot be accurately understood in the absence of a full quantitative understanding of the influence of resting metabolism and its variability across individuals.

At the close of the award period, we had greatly improved and refined our height-weight-speed model for predicting walking metabolic rates. Doing so also advanced our efforts to develop an aerobic fitness assessment procedure that relies on our walking model and steady-state heart rates. The procedure requires only a brief walking test of roughly five minutes.

We also had a manuscript accepted on high-speed running that was made possible by the support provided over the course of the award. Our work on refinements to our walking model also continues using the literature-based approach described in prior reports.

A working schematic of our Height-Weight-Speed model appears below in Figure 1. Some of the results following in this report have been presented below were provided in prior reports. Previously, our stature-inclusive metabolic model is performing well, accounting for 94% of the variability in walking metabolic rates between individuals and across speeds per the illustration in Figure 2 (with an SEE of $1.07 \text{ mls} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$).

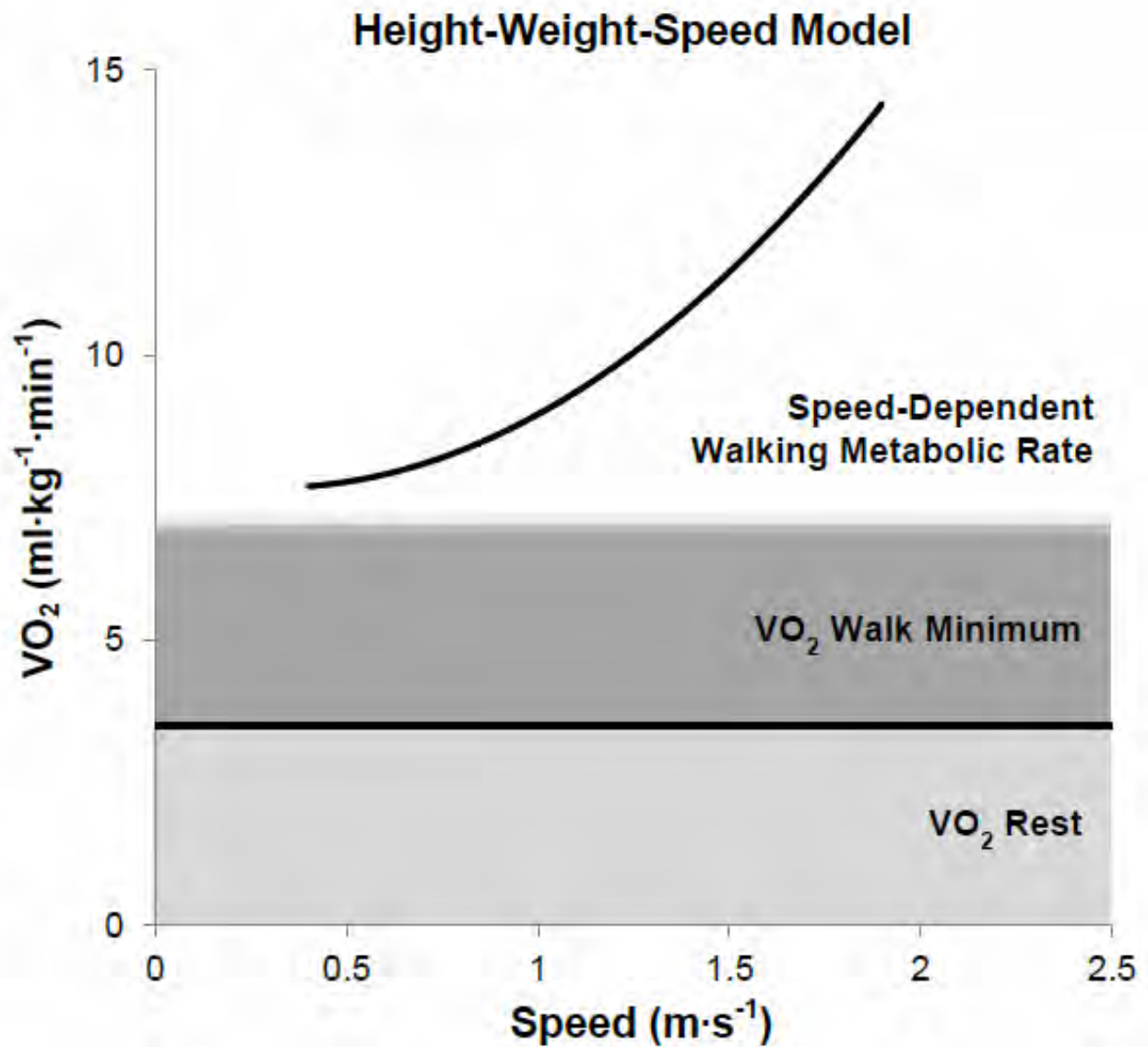


Figure 1. The Height-Weight-Speed model of walking metabolism; the above schematic illustrates the theorized metabolic components of walking metabolism in relation to walking speed. The model provides accurate predictions of metabolic rates during level walking from height, weight and walking speed.

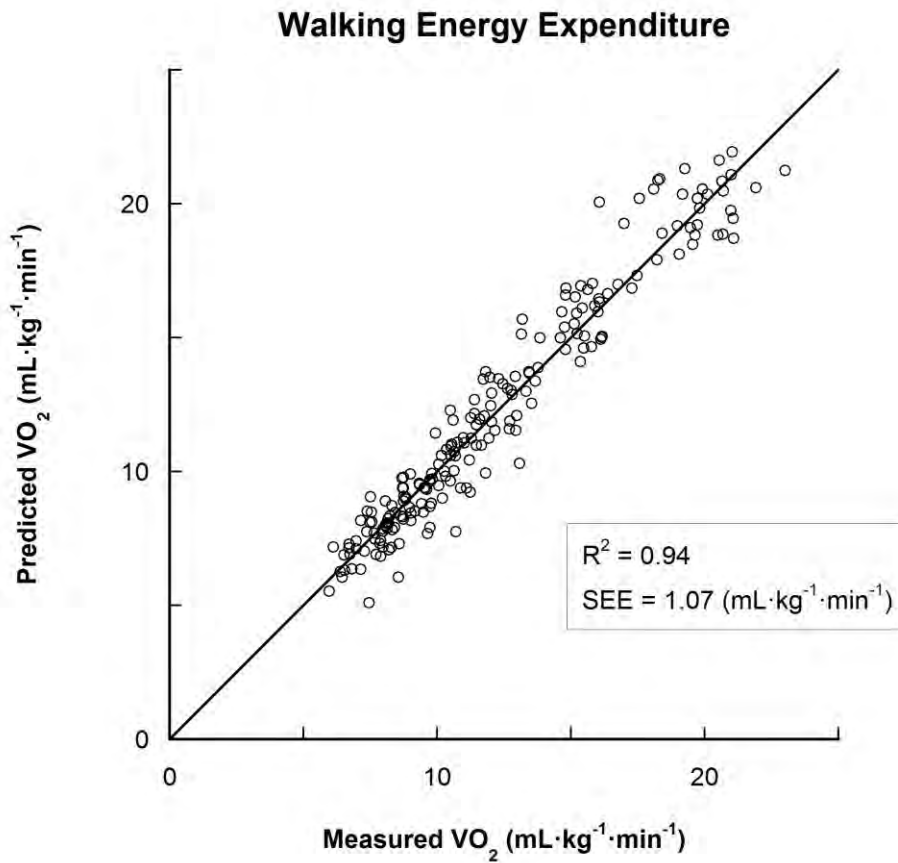


Figure 2. The agreement between measured and predicted rates of oxygen uptake (n=34 subjects) at six different treadmill walking speeds from 0.4 to 1.9 meters per second.

Also, per prior reports, we have had 21 subjects complete a three-speed protocol on level asphalt with metabolic measurements being acquired using the Douglas bag technique. The agreement between the treadmill data from the laboratory and the over-ground data for these subjects is illustrated in Figure 3 below.

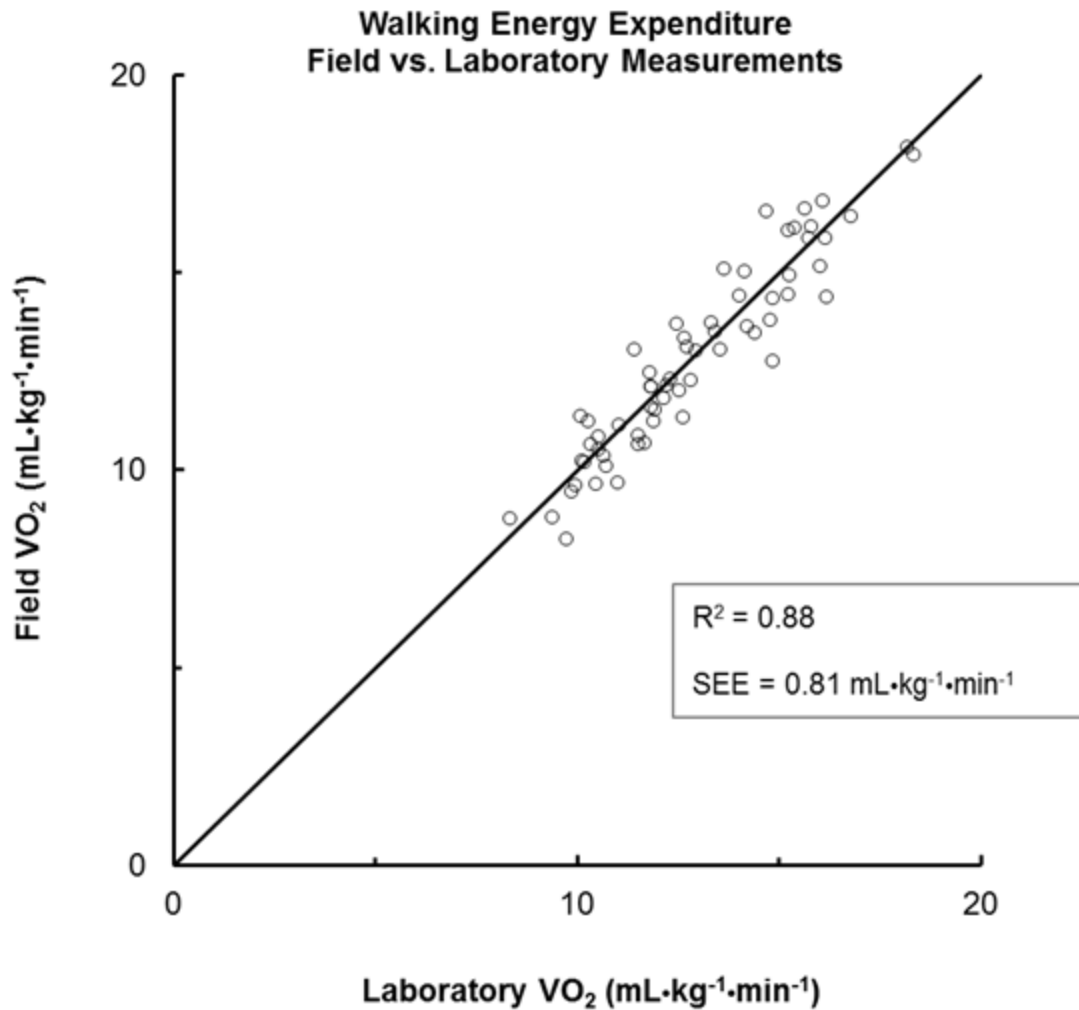


Figure 3. The agreement between treadmill and over-ground rates of oxygen uptake ($n=21$ subjects) at three walking speeds: 1.0, 1.3 and 1.6 meters per second.

The predictions provided by our stature-based model on the over-ground pavement trials thus far completed appear below in Figure 4.

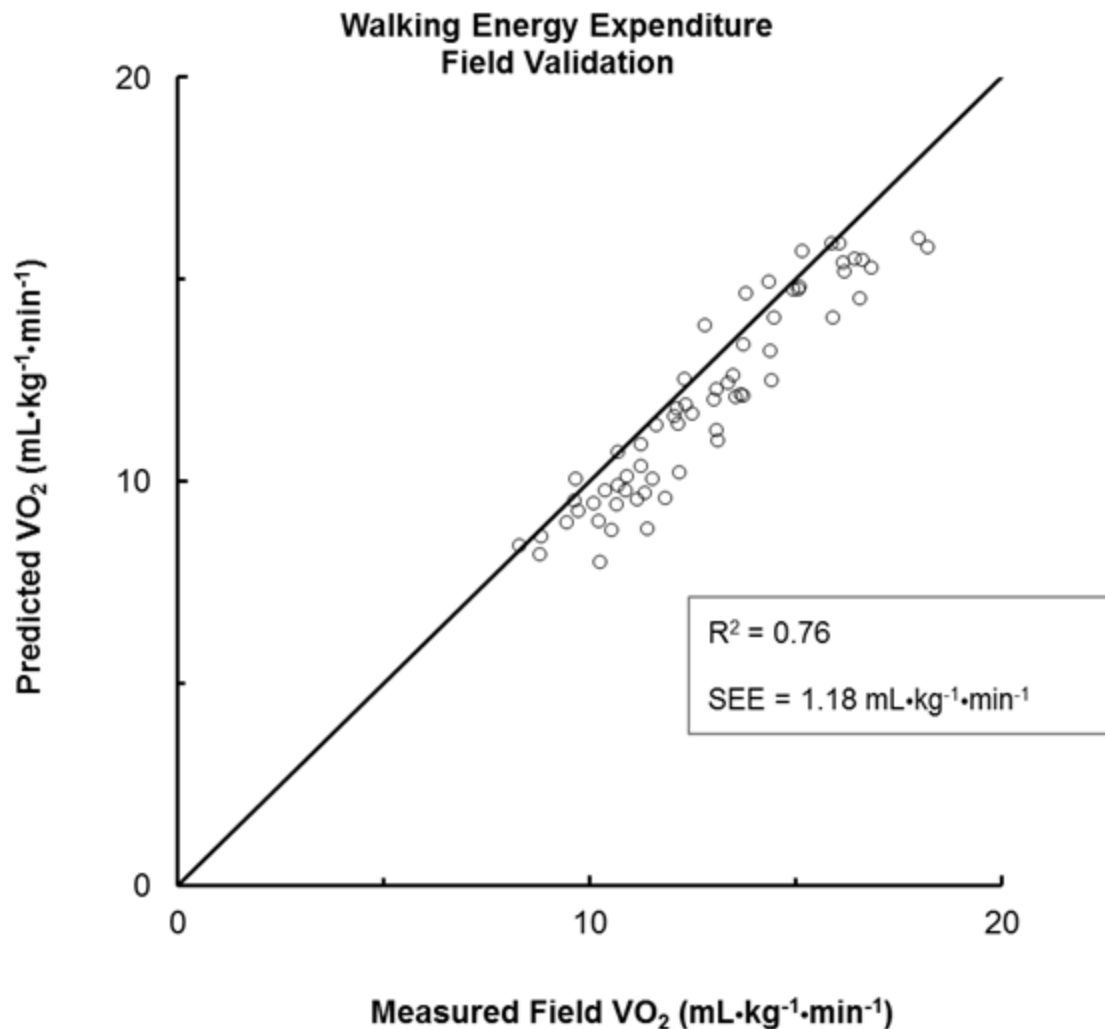


Figure 4. The agreement between measured rates of oxygen uptake (n=21 subjects) during over-ground walking on pavement at 1.0, 1.3 and 1.6 meters per second vs. the rates predicted by our stature-based model.

Also, per prior reports, we present the condition-agreement of the walking metabolic rates of the 10 subjects who completed both treadmill and grass-field testing below in Figure 4. We found that walking on grass elevated the metabolic cost of walking by 5-10% with a slight speed-dependency. Therefore, our treadmill-based model under-predicted the metabolic rates measured on

grass. However, the re-optimized model does provide a good fit to the grass data per the figure.

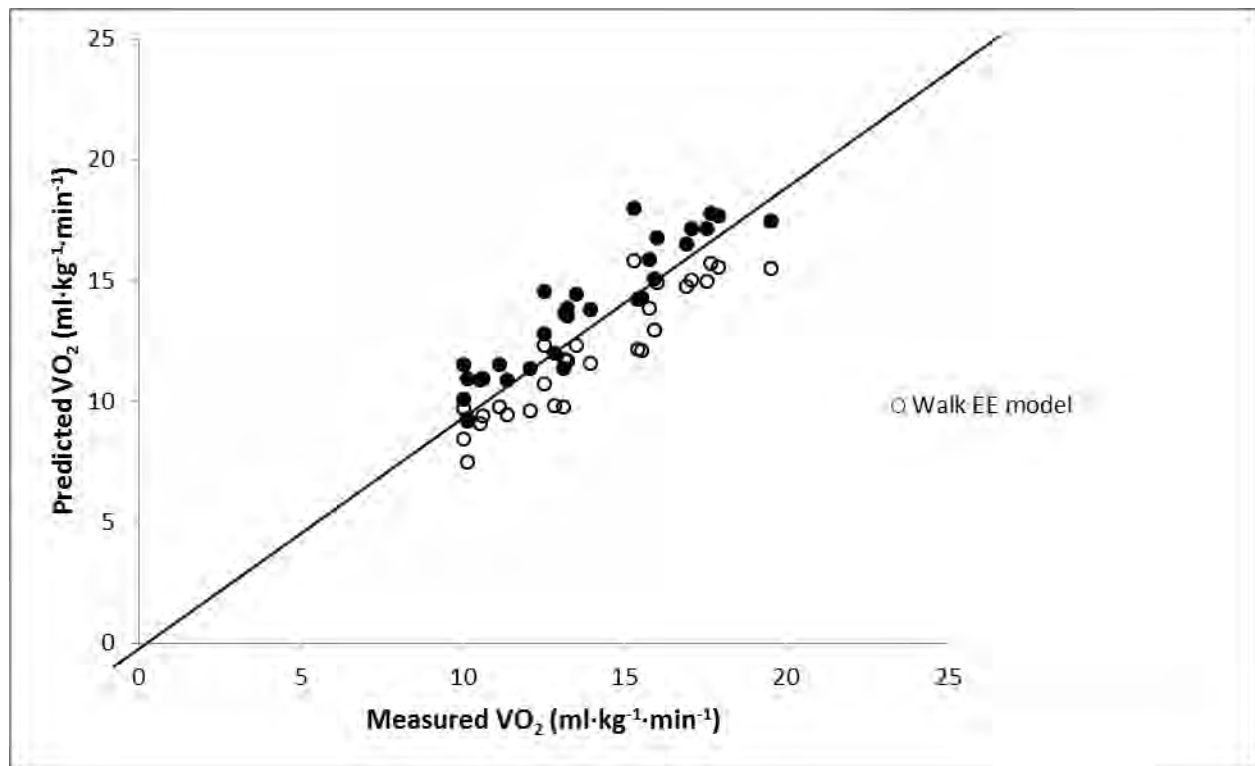


Figure 4. The agreement between measured rates of oxygen uptake (n=21 subjects) during over-ground walking on pavement at 1.0, 1.3 and 1.6 meters per second vs. the rates predicted by our stature-based model.

In the coming months, we will continue to refine our walking model and algorithm for predicting aerobic fitness from a walking protocol. The primary current focus is on the first of the two predictive steps of our walking metabolism model. In the latter portion of the project, we have compiled literature data to supplement our original data to better evaluate the validity of the model. The literature data set was compiled to include a broad range of heights, weight and walking speeds. The data set includes 129 population means for walking metabolism. These means were compiled from groups with disparate mean height and weight values.

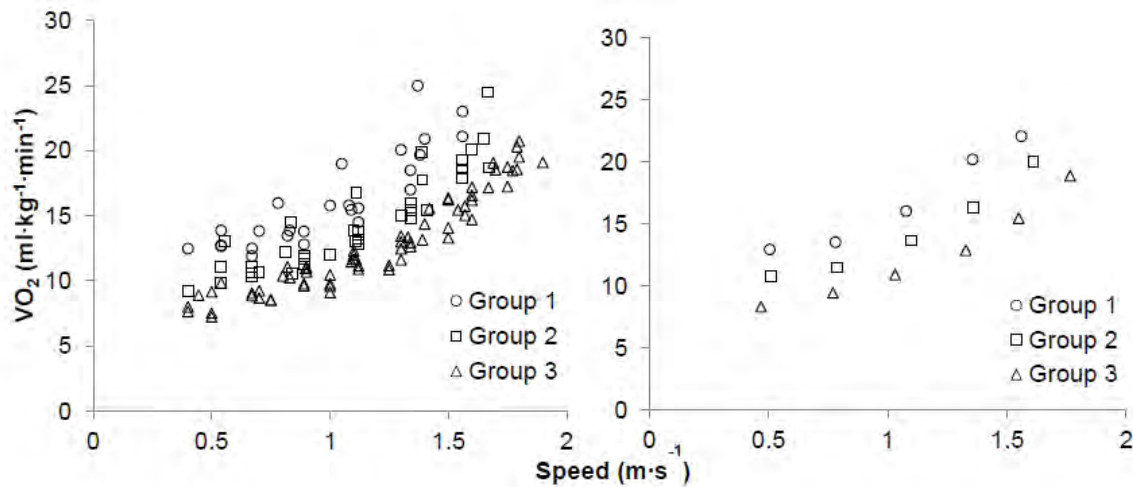


Figure 5. Rates of oxygen uptake vs. speed during unloaded walking (panel A, n=129). Each data point represents the mean value acquired from a population of subjects walking on a firm level surface. The data set includes both over-ground and treadmill data. The three symbol types for group 1 (circles), group 2 (squares) and group 3 (triangles) are for short, medium and tall subjects. The overall mean values for all the subject groups within the three respective height ranges appear in panel B.

Per our last report, we are also attempting to develop simplified approaches to predicting resting metabolic rate based on specific power equations that require only body mass and sex. These relationships are important for practical prediction of the gross metabolic rates during walking since the resting fraction of the total is typically one-third.

The above analysis is being prepared to further develop and refine our model of walking metabolism per above. This work remains in progress but this portion is close to completion. The literature acquisition approach has proven to be a critically effective approach for further development, validation and refinement of our walking metabolism model.

Our procedural approach to the literature test and refinement of the model was as follows:

Experimental Design: We adopted a literature compilation approach to evaluating the relative accuracy with which different models predict human walking metabolism for several reasons. First, the existing literature is now sufficiently expansive to comprehensively incorporate the influences of height, weight, and speed on walking metabolic rates. Second, the use mean data from small-populations, rather than individual values is likely to insulate the analysis from the skewing effects individual

outliers and aberrant data points can have. Third, the aggregation of means from many studies should mitigate measurement or condition-specific error from individual studies.

Fourth, the use of older, well-established studies should ensure the relative validity of the population means included. Finally, contemporary digitizing techniques allow data published in graphic form to be extracted with a high degree of accuracy. Collectively, these factors should allow for the aggregation of a robust and powerful data set for investigating the energy cost of level human walking.

Hypothesis Tests One and Two: Based largely on the prior results reported on 78 individuals who spanned a broad range of body sizes, we expected the following two hypothesis test outcomes. First, we expected that the error of prediction (SEE) would, on average, be twice as large when the walking portion of the body's total metabolic rate was modeled with one non-resting metabolic component rather than two. Second, we expected that the error with which the aggregated literature means would be predicted by the ACSM and Pandolf et al. equations would be two times larger than the corresponding error of prediction of the HWS model equation, again using the standard error of estimate (SEE) statistic. Further, as a general standard for goodness of fit (i.e. accurately capturing both speed and size variation) we set a rough a priori threshold of $R^2 \geq 0.90$.

Data Set Criteria: Our literature data set was strategically aggregated to fully encompass the influences of height, weight, and speed on human walking metabolism. The criteria determining whether the literature values available qualified for inclusion were as follows. First, the mean height and weight of the group had to be reported in the original work. Second, metabolic means from a sufficient number of speeds to provide a minimum value for the energy expended per unit distance, or metabolic cost of transport, also needed to be available. Third, to avoid speeds in the walk-run transition range that were too fast to be true walking speeds, we implemented a standardized maximum-speed cut-off using an analogue of the Froude number:

$$Fr = \frac{\text{walking speed}}{\sqrt{g \cdot (ht \cdot 0.52)}} \quad (1)$$

where walking speed is in units of $\text{m} \cdot \text{s}^{-1}$, height is in meters, and g is the gravitational constant in $\text{m} \cdot \text{s}^{-2}$. The Froude number is widely used to quantify speeds that are equivalent for walkers and runners who differ in body size. The standard Froude index does so using leg length. Here, as previously, we used a Froude

number analogue that substitutes height for leg length because studies on walking metabolism generally report the height means of the groups tested, but often do not report leg length. Finally, we did not include data from individuals ≥ 65 years of age because the metabolic cost of walking is elevated in elderly subjects (Ortega and Farley, 2007) for reasons that have not yet been identified.

Digitizing Process: Group mean values were acquired from the tables or figures in prior publications. Those data points acquired from figures were digitized in accordance with the highly accurate techniques now available (Sistrom & Mergo, 2003; de Oliveira et al., 2003). Original illustrations were enlarged and oriented on a grid to allow precision vertical and horizontal line fits to the data point of interest. Line fits were extended to the X- and Y-axes to determine the x and y values for each data point. Data point values were also determined using an automated digitizer (Web Plot Digitizer, Rohatgi, 2013).

Data Set Characteristics: Using the inclusion criteria specified, our literature search from the early 1900's to the present yielded 25 subject groups from 10 publications spanning a 50-year period from 1960 to 2010. The number of subjects per population group ranged from 5 to 42. Age means ranged from 5.2 to 40.7 years, height means ranged from 1.03 to 1.82 meters, and body mass means ranged from 18.9 to 78.0 kilograms.

Walking Metabolism Models: The specific forms of the one- and two metabolic components used to model the walking, or non-resting portion of gross walking metabolism, were guided by both the primary literature traditions and our recent modeling efforts. Our recently introduced HWS model of walking metabolism appears schematically in Figure 1. Mass-specific rates of oxygen uptake appear on the Y-axis, while walking speed appears on the X-axis. The two non-resting components into which this model partitions walking metabolic rates are a minimum walking metabolic rate, and a speed-dependent metabolic rate. Partitioning gross or total metabolic rates into a baseline component that corresponds to resting metabolic rate and an exercise component is a common practice. However, the HWS model is atypical in dividing the walking component of the body's total metabolic rate into two aforementioned components: a constant, predominantly postural component and a second speed-dependent component. The novel component of the HWS model, the minimum walking metabolic rate, describes the support and postural costs of the walking movement and is independent of walking speed. The speed-dependent component quantifies the simultaneous influences of walking speed, height, and gait mechanics as previously described. The

HWS model incorporates body mass into the denominator of each metabolic component and takes the following form:

$$\begin{array}{c}
 \text{VO}_{2\text{-gross}} = \text{VO}_{2\text{-rest}} + \underbrace{C_1 \cdot \text{VO}_{2\text{-rest}}}_{\text{Minimum Walking}} + \underbrace{(C_2 \cdot V^{\text{exp}}) \cdot \text{Ht}^{-1}}_{\text{Speed-Dependent}} \\
 \underbrace{\text{VO}_{2\text{-rest}}}_{\text{Resting Metabolism}} \quad \underbrace{\text{Minimum Walking} \quad \text{Speed-Dependent}}_{\text{Walking Metabolism}}
 \end{array}$$

where $\text{VO}_{2\text{-gross}}$ is the body's total rate of oxygen uptake, $\text{VO}_{2\text{-rest}}$ is the body's supine resting rate of oxygen uptake, C_1 is a coefficient that describes the minimum walking rate of oxygen uptake as a multiple of the resting rate, and C_2 is a coefficient describing the speed-dependent increases in the rate of oxygen uptake as a function of walking velocity, V , raised to the exponent, exp , divided by the height (Ht) of the individual. Hence, the sum of the model's second and third components represents the metabolic rate attributable to walking ($\text{VO}_{2\text{-walk}}$).

All the terms in Eq. 1 are expressed in mass-specific units of oxygen uptake of $\text{mls O}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$ in accordance with literature convention. Per our scientific objectives, Fig. 1, Eq. 1 and our previous work, the term metabolic rate is used to refer to mass-specific rates of oxygen uptake throughout.

Resting Metabolic Rates: The resting portion of the gross or total walking metabolic rates in our literature data set was determined on the basis of height, weight, gender and age for each of the 25 population means using the prediction equations of Schofield et al. These equations have been extensively validated and are known to predict resting metabolic rates with a high degree of accuracy, typically in the range of $0.5 \text{ mls O}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$ (Input refs from Walk EE methods). Because all of the predictive models tested incorporated the same Schofield-derived RMR quantity, this portion of the total or gross metabolic rate attributed to RMR was held constant across all the model types tested.

Modeling Iterations, Analyses and Equations. Models of three basic forms for describing the metabolic rate vs. walking speed (V) relationship were evaluated: linear ($\propto V^{1.0}$), exponential ($\propto V^{2.0}$) and exponential with an inverse relationship to height ($\propto V^{2.0}/\text{Ht}$). For each of three model types, both one- and two-component versions were derived. The procedures used to

determine the best fits of these model forms to the literature data set are described below.

Model Best-fit Procedures: For each of the three basic model forms, separate model versions were derived, a first that treated net walking metabolism as a single entity, and a second that partitioned walking metabolism into two components: a constant, largely postural component and a separate speed-dependent component in accordance with the schematic in Figure 1. For consistency and ease of interpretation, the postural component of walking metabolism was modeled the same way across all three model types, specifically as a multiple of the RMR, therefore equal to the quantity: $C_1 \cdot \text{RMR}$ per the above equation.

In order to maximize the fit of each model to the population mean values in the aggregated literature data set, coefficients were derived that provided the best fit (i.e. highest R^2 value) across the 127 values included. The coefficient describing the minimum walking metabolic rate (C_1) in the two component models, and the coefficient describing the speed-dependent walking metabolic rate (C_2) in all models were optimized to minimize the sum squared error values. The optimizer function in Excel was used as previously described (Weyand et al, 2013) due to its ability to optimize a coefficient while holding other values, such as estimated resting metabolic rate, walking velocity, and height fixed at their known values (Fvlstra et al. 1998; Microsoft Excel Solver, Excel 2010 version). Equations in each of the six model forms were optimized to best fit walking VO_2 values for the literature data set.

In order to maximize predictive accuracy of a given equation, coefficients were derived such that the fit of the predicted data most closely matched the data points pulled from the literature sources (i.e. highest R^2 value) across the wide range of height, weight, and walking speeds. The coefficient describing the minimum walking metabolic rate (C_1) in the two component model, and the coefficient describing the speed-dependent walking metabolic rate (C_2) in all models were optimized to minimize the sum squared error of prediction. The optimizer function in Excel was used due to its ability to optimize a coefficient while holding other values, such as estimated resting metabolic rate, walking velocity, and height fixed at their known values (Fvlstra et al. 1998; Microsoft Excel Solver, Excel 2010 version). Once best-fit equations were derived, they were used to predict walking VO_2 values for all 127 literature data points and subsequently plotted against walking speed.

We also tested a 7th predictive model in which the minimum walking metabolic rate was treated as a constant absolute value across all group means rather than being modeled as a multiple of

the group-specific RMR values. In this case, the equation was comprised of resting metabolic rate, a coefficient (C_1), and a coefficient (C_2) times walking velocity squared divided by height.

Data Set Categorization by Stature: The 127 values for small population group-mean metabolic rates in our aggregated data set appear in Figure 5A as a function of walking speed. The influence of height on gross walking metabolic rates led us to classify these values by stature, using a three category scheme of: short, intermediate, and tall. These stature classifications were not necessary for, and indeed were not part of, our formal hypothesis tests. Rather, we implemented these classifications to allow for visual evaluation of whether the different models tested fit the walking energy expenditure values equivalently across the different stature means present in the data set, or were biased toward shorter or taller individuals (Table 2). The stature means of the populations in the short, intermediate, and tall groups were: 118.0 ± 3.6 , 141.0 ± 2.4 , and 171.5 ± 1.9 cm, respectively.

Also, for graphical purposes we determined representative metabolic rate vs. speed relationships as follows. Within each height classification group, we averaged the literature metabolic rate data points acquired to determine values at or near 5 speeds: 0.5, 0.8, 1.0, 1.3, 1.6 and $1.8 \text{ m}\cdot\text{s}^{-1}$. The exact speeds for the respective height groups varied slightly in accordance with the different protocol speeds administered in the different literature sources. This process allowed us to formulate trend lines for the metabolic rate vs. speed that corresponded to the literature values for each of the three respective height classification groups (Figure 5B). These trend lines were formulated to provide visual references to assess how well the best-fits derived for each of the six different model forms we tested accounted for the stature and speed-related variation present in the metabolic rate means in our aggregated literature data set.

Predictive Accuracy - Height-Weight-Speed Model vs. ACSM & Pandolf et al.: In addition to evaluating the accuracy of the equations derived here using the model forms already described, we also evaluated how accurately three previously published equations were able to predict the 127 mean values in our literature aggregated data set. Per the forms of the three respective equations provided, literature values were predicted using the ACSM and Pandolf et al. equations on the basis of walking speed only. For the HWS model, literature values were predicted using walking speed, estimated RMR, and the mean height of each population group. The agreement between the actual

values across the three equations was evaluated using both the R^2 statistic and SEE.

Aerobic Fitness Index Results: In addition, many of the subjects who were tested for the further development of our stature-based model of walking energy expenditure have also completed maximal metabolic rate tests. Per our previous report regarding these data, we have further developed the two-step algorithm to estimate maximal aerobic power from submaximal heart rates. As per our last reports, our current algorithms predict maximal aerobic power with an average accuracy between 8.0 and 10.0% for fully independent predictions on the 51 individuals currently included in the analysis (VO_{2max} range = 19 to 75 $mls \cdot kg^{-1} \cdot min^{-1}$).

Our average absolute error for these predictions currently stands 4.39 $mls \cdot kg^{-1} \cdot min^{-1}$, and our working SEE is 5.62 $mls \cdot kg^{-1} \cdot min^{-1}$. We have note re-optimized to incorporate the subjects who were tested most recently.

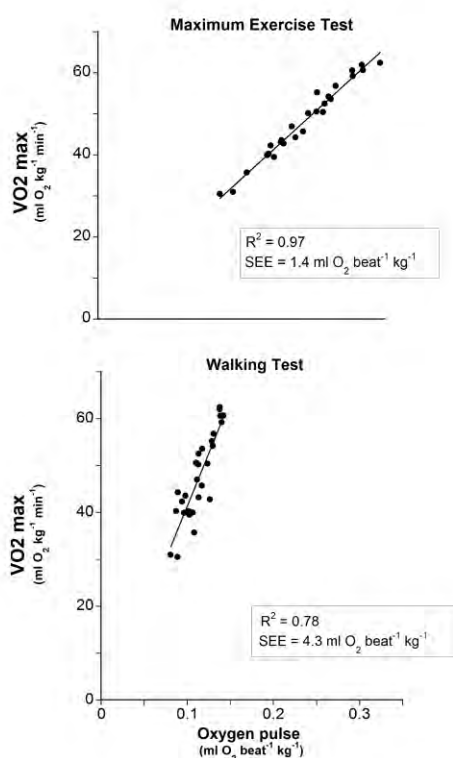


Figure 6. Measured rates of maximal oxygen uptake (VO_{2max} , Y-axis) vs. the measured oxygen pulse (O_2 per heartbeat at VO_{2max}) appear in the uppermost panel. The lower panel also illustrates the same measured maximal oxygen uptake (VO_{2max} , Y-axis) vs. the estimated oxygen pulse during submaximal treadmill walking. The submaximal oxygen pulse relationship provides the basis for our walking test of aerobic fitness.

KEY RESEARCH ACCOMPLISHMENTS:

- 1) Considerable advancement in the understanding of walking metabolism has been realized through testing of our walking metabolism model (also called the Height-Weight-Speed model).
- 2) Successful level over-ground tests of the walking model have been completed on two different terrain types: pavement and dry grass.
- 3) Tests of resting, walking and maximal aerobic metabolism have been completed on a relatively large cohort of subjects.
- 4) The Height-Weight-Speed model has been published after completion of a rigorous cross-validation procedure.
- 5) A one-of-a-kind literature data base on human walking metabolism that includes over-ground and treadmill walking has been compiled and used to advance the Height-Weight-Speed model.
- 6) A procedure and algorithms have been developed to predict maximal aerobic metabolism from measured, steady-state submaximal heart rates and estimated oxygen uptake and oxygen pulse.
- 7) Two walking metabolism manuscripts have been published; one abstract has been published (Weyand et al, 2010; Weyand et al, 2013), and a third full manuscript (the literature validation of the Height-Weight-Speed model) will be submitted shortly.
- 8) One physical performance manuscript, incorporating work from an earlier phase of the award has been published (Bundle & Weyand, 2012).
- 9) An aerobic fitness index invention disclosure was submitted for internal consideration by SMU for a possible patent application (consideration is ongoing).
- 10) Load carriage experiments and advances in our walking metabolism model have led to a major award to investigate and quantify the influence of load on locomotor metabolism and running performance [W81XWH-12-2-0013, Locomotion with loads: practical approaches to predicting performance outcomes, \$892,000].

REPORTABLE OUTCOMES:

Please see key research accomplishments above.

Personnel receiving salary support from the project included: Peter Weyand, Laurence Ryan, Nicole Schultz, Lindsay Wohlers, Kenneth Clark.

CONCLUSIONS:

Our results have substantially advanced the basic understanding of walking metabolism with important basic and applied outcomes. Basic outcomes include an advanced understanding of the determinants of walking energy expenditure. Applied benefits include, but are not limited to: the ability to predict walking metabolic rates on firm level surfaces from only height, weight and walking speed, whether via direct measurements or monitoring via personal sensors, and the ability to estimate aerobic fitness tests from measured heart rates and estimated rates of oxygen uptake and oxygen pulses are feasible.

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APPENDICES:

Per the reporting instructions, three manuscripts have been included in the appendix below. In order, these are:

Bundle M, Weyand P. Sprint exercise performance: does metabolic power matter? *Exercise and Sport Science Reviews*, **40**: 174-182, 2012.

Weyand P, Smith B, Payau M, Butte N. The mass-specific energy cost of human walking is set by stature, *Journal of Experimental Biology*, **213**: 3972-3979, 2010.

Weyand P, Smith B, Ludlow L, Schultz N, Puyau M, Butte F. Predicting metabolic rate across speed: one fit for all body sizes? *Journal of Applied Physiology*, **115**: 332-342, 2013.

One abstract was published:

Wohlers, L. Clark K, Ryan L, Weyand P. High on grass: the influence of terrain on human walking economy. Texas American College of Sports Medicine, 2013.

Sprint Exercise Performance: Does Metabolic Power Matter?

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Summary

Sprinting performance is determined by the application of musculoskeletal forces that are rapidly compromised by rates of *in vivo* fatigue.

Abstract

Prevailing physiological paradigms explain both sprint and endurance exercise performance in terms of the availability of metabolic energy. However, for all-out efforts ≤ 60 seconds the prevailing view is no longer viable. Contemporary evidence indicates that sprinting performance is determined by musculoskeletal force application, with a duration-dependency explained by the intrinsically rapid rates at which skeletal muscle fatigues *in vivo*.

Keywords: Force application, skeletal muscle, *in vivo* fatigue, locomotion, biomechanics

Introduction: Time-Dependent Engines

Imagine purchasing a new sports car and taking it to an empty highway for a performance test. With nothing but open road ahead, you put the gas pedal all the way to the floor. In a matter of seconds, the transmission shifts, the engine revs, and the vehicle accelerates to attain a maximum velocity of 200 kilometers per hour. However, as you settle in at full throttle with the expectation of sustained speed, the engine suddenly begins to lose power. The power losses are rapid at first, but become more gradual over time. Eventually, your new engine steadies out with only enough power output to sustain a relatively slow velocity between 50 and 100 kilometers per hour.

As odd as the preceding scenario seems in the context of a man-made engine, from a mechanical and temporal standpoint, this is precisely how the muscular engines of humans and other animals perform. Even though natural and manufactured engines can be similar in relying on chemical energy to generate force and power, their performance-duration relationships are strikingly dissimilar. Thus, we quite naturally expect automobile and other man-made engines to perform without fatiguing, but the biologically equivalent prospects of an elite human sprinter finishing a mile run in just over two minutes, or a cheetah galloping through 26 miles in less than half an hour, do not seem remotely possible. Yet the respective top speeds of these two athletes, if sustained, would permit these performances.

Rather, personal experience and observation lead us to expect rapid decrements in performance capabilities anytime the duration of a maximal physical effort becomes more prolonged. The duration-dependency of performance that has been well-characterized for humans and other animals appears in general form in Figure 1. As illustrated by the negative exponential nature of the relationship, the greatest decrements in performance occur across those efforts that span the briefest durations. For example, the decrements that occur as effort durations extend from 2 to 30 s are much larger than those that occur with duration increases from 30 to 60 s, and those that take place from 60 to 120 s. This pattern of exponential decrease continues until durations extend to between five and ten minutes where performance falls to the levels that can be well sustained by the body's renewable, aerobic sources of energy (13). Thereafter, performance decrements become relatively small, even as durations extend out to several hours.

Here, we consider the mechanical and metabolic factors responsible for the duration-dependency of biological engines. We start with the mechanics that directly determine performance during burst sprint activities of a few seconds or less, and then consider how these requirements change as sprint durations increase. We also

evaluate the prevailing view that the duration-dependency universally observed for biological engines results from the availability of chemical energy to provide fuel to the active muscles. Although this view has been largely unchallenged in the last half century, reconsideration is warranted given more extensive evidence now available.

Our analysis draws largely on the all-out running speeds and cycling power outputs of humans because of the extent and quality of the data available, and because the mechanical and metabolic contrasts between these two exercises provide informative scientific insights. Although we rely heavily on the experimental evidence from these two modes of human sprinting, we expect our conclusions to generalize to non-human species and any activity that engages a large fraction of the body's musculature for basic biological reasons. The structural and functional properties of the musculoskeletal system are largely invariant across species (11, 26) as are the pathways of chemical energy provision within skeletal muscle (15). Our analysis will focus on all-out efforts in the non-sustainable range of durations of up to roughly five minutes, with a particular emphasis on those efforts lasting less than a single minute. We have focused on the duration range in which performance decrements are greatest to provide the most rigorous evaluation of existing scientific ideas.

The Mechanical Basis of Sprinting Performance: External Force Application

In the simplest terms, performance can be analyzed considering either the input to, or the output from, the skeletal muscles that serve as biological engines: the input being the chemical energy that fuels muscular contraction and the output being the force or mechanical power that the contractions produce. Generally, performance in both sprint and endurance events has been causally attributed to the chemical energy input while the musculoskeletal mechanics that determine bodily motion and performance have been regarded as a dependent entity (8, 9, 14, 16-18, 22, 27, 28). This conceptualization evolved from the original analysis put forth to explain the performance-duration relationships of human, canine and equine athletes by A.V. Hill early in the last century (10). In nearly a century since Hill's analysis, robust empirical support has emerged for the endurance, but not the sprint portion of the curve (24). The considerable difference in experimental support is attributable, at least in part, to measurement capabilities. The chemical energy available to the body from aerobic metabolism that fuels endurance efforts can be accurately quantified by measuring oxygen uptake at the mouth, but an equivalent technique for measuring the anaerobic chemical energy also released during sprint efforts does not presently exist. Thus, two primary factors have

contributed to the original and ongoing acceptance of the view that sprint exercise performance is limited by the metabolic energy available: 1) how well metabolic models explain endurance performance (8, 13, 22), and 2) the absence of data to refute them.

We have opted to deviate from the classical approach by focusing on the mechanical output of the musculoskeletal system that can be measured rather than the chemical energy input that cannot. The understanding of the relationships between force, motion and performance provided by classical Newtonian mechanics support the viability of this approach. From respective whole-body mechanical entities provided by the external forces applied, either running speed or cycling power output, simple, quantitative performance relationships have been put forth (5, 34, 35):

$$\text{Spd} = \frac{F_g}{F_{wb}} \cdot L_c \cdot \text{Freq}_{\text{step}} \quad (\text{eq. 1})$$

$$P = F_p \cdot L_{ds} \cdot \text{Freq}_{ds} \quad (\text{eq. 2})$$

Where Spd and P represent running speed and cycling mechanical power output, F_g/F_{wb} and F_p represent the external applied forces; for running the stance-averaged vertical ground force as a multiple of the body's weight and for cycling the average down-stroke pedal force. The length terms, L_c and L_{ds} , represent the forward distance through which the body travels while the foot is in contact with the ground during running and the distance through which the pedal force is applied during each cycling down-stroke (i.e. one-half of the pedal circumference). Finally, the frequency terms, $\text{Freq}_{\text{step}}$ and Freq_{ds} , are the inverse of the step time and down-stroke times, where the former is defined as the sum of one contact and one aerial period.

These force-performance relationships have several features that should be noted. The running equation does not include the horizontal component of the ground reaction force because these forces are relatively small and contribute limitedly to the magnitude of the total ground reaction force during constant-speed sprint running without wind resistance (34). Our cycling equation does not include the condition-specific factors that introduce variability into the over-ground power-speed relationship. Additionally, the forces determining performance are mass-specific for the exercise that is weight-bearing (eq. 1) and absolute for the exercise (eq. 2) that is not.

The general relationship between the external forces the skeleton applies to the environment and the level of performance attained is illustrated in Figure 2A+D. The forces appearing in the figure represent those typical of

athletic subjects tested in the two primary modes of sprinting examined here. In both cases, the threshold separating sustainable and non-sustainable forces occurs at the minimum level of mechanical performance that can be supported by the maximum rates of aerobic metabolism. Note that while the maximum rate of aerobic metabolism available to support external force application in these two exercises is virtually the same, (6, 33) the relative forces, timing of force application, corresponding rates of energy utilization, and the relative intensities attained are not (Fig. 2B, C, E, F). During running, the aerobic power of well-trained subjects can typically sustain ground forces that are twice the body's weight, and 75-85% of those applied during a top speed sprint. In contrast, the pedal forces that can be sustained by the same level of aerobic power during cycling are only one-fourth of the body's weight and only 25-35% of those applied during a burst cycle sprint when peak power output is achieved.

However, in both exercises, the force-performance relationships presented in Figure 2 are reasonably linear across the full range of endurance and sprint exercise intensities. These close force-performance relationships result from limited variation in the length and frequency terms in our respective force-performance equations. Specifically, running contact lengths are a narrow function of leg lengths and exhibit little variation as runners increase from their intermediate to top sprinting speeds (34, 35). Cycling down-stroke lengths are mechanically fixed by crank dimensions that are largely standardized across different bikes and riders. Similarly, the respective stride and pedal frequencies that maximize burst sprint performances exhibit modest variation between individuals during running (35), and almost no variation during cycling (19). Thus, for both exercises, differences in sprinting performance are predominantly a function of the magnitude of the external forces applied because length and frequency variation is limited.

In addition to the deterministic relationship between external force application and performance, external forces also appear to be reasonably representative of the extensor muscle forces required. The data currently available from techniques that estimate the minimum net extensor forces acting across the joints of the limb suggest that the relationship between the external forces applied and the net muscle forces generated across the joints most relevant for performance is relatively constant. During running, the ankle and knee extensors generate forces that are roughly two to three times greater than the ground forces applied (3). During cycling, the knee and hip extensor forces are roughly three times greater than the pedal forces applied (3, 12). Accordingly, within each mode, the

external forces applied during sprinting appear to be consistently related to the corresponding muscle forces regardless of the intensity or duration of the effort.

Neural Control and Maintenance of Force Application

The recognition that sprinting performance and its duration-dependency are directly set by the external forces applied to the environment begs two questions of immediate relevance. First, what determines the maximum external forces that the musculoskeletal system can apply during brief, all-out burst-style sprints? And, second, why do the external forces applied become progressively smaller as the duration of sprinting increases, even though the effort being put forth is maximal? In the first case, an understanding of the factors determining the maximal dynamic limb extensor forces that can be applied, particularly during sprint running, remains to be established (34). In the second case, insight into the mechanisms of force impairment can be gleaned from the patterns of neuromuscular activation observed during all-out sprint trials.

Selecting and maintaining the external forces needed for a sprint trial of any given intensity requires a fairly precise mechanism for controlling muscle force generation. Force outputs are regulated primarily by the number of motor units and therefore muscle fibers activated, and secondarily by frequency modulation within the activated units (4, 29). Experimentally, the levels of neuromuscular activation resulting from both neural control mechanisms can be assessed by surface electromyography (EMG) to measure the electrical activity resulting from membrane depolarization of the activated muscle fibers. For both static and dynamic contractions requiring similar limb positioning and relative shortening velocities, external force application is directly related to the rectified and integrated EMG signal (4). As can be seen in Figure 3A, for the vastus lateralis muscle that extends the knee, the EMG-external force relationship is linear over a 6-fold range of pedal forces from 100 to 600 N at a pedal cadence of 100 rpm when fatigue is not present.

With this relationship in place, we next considered the neuromuscular activity-external force relationship across the full time course of all-out sprint trials of different intensities. For both the sprint cycling and running, trials to failure were administered at constant intensities to hold the external and joint extensor forces required relatively constant. Three sprint cycling trials (Fig. 3B) were administered with pedal forces exceeding 300 N, and therefore in the non-sustainable force range for this individual, with the fourth being administered at a sustainable

force level of 100 N. The sprint running trial in Figure 4 was administered at a non-sustainable treadmill running speed of 7.3 m/s. For all three of the sprint cycling trials in Figure 3B, the EMG activity of the vastus lateralis muscle increased continuously to maintain the constant pedal forces the trial required. Similarly, during the sprint running trial, the EMG activity of the extensor muscles monitored increased continuously throughout the 47 s trial illustrated while the ground forces remained relatively constant (Fig. 3C+D). In contrast, in the non-sprint cycling trial that required relatively low, sustainable pedal forces, the EMG activity remained essentially constant over the course of the trial.

The EMG data provide several conclusions regarding the maintenance of the external forces applied during all-out sprinting. First, for all the sprint cycling and running trials examined, the levels of neuromuscular activation needed to maintain a constant external force increased continuously from the outset to the conclusion of the trial. Second, the rates of increase in the compensatory neuromuscular activity observed were typically more rapid for the briefest trials requiring the greatest forces. Third, no increases in neuromuscular activity were observed when the force required was sufficiently small to be supported by aerobic metabolism. And, fourth, the levels of neuromuscular activation at the point of trial and force failure were lower for the longer duration sprint trials that required lesser forces.

These relatively simple neuromuscular experiments indicate that all-out sprinting performances are highly duration-dependent because of the rapidity of musculoskeletal fatigue *in vivo* during dynamic exercise requiring large force outputs. The timing and intensity-dependent nature of the force impairment observed complements the functional understanding of muscle force production at both the systemic and cellular levels. In the former case, fatigue as indicated by compensatory neuromuscular activity occurs more rapidly in those sprints that require greater external forces which activate and rely on faster, more fatigable muscle fibers (1, 4, 29). In the latter case, the virtually instantaneous, and intensity-dependent nature of the fatigue observed is consistent with a cellular level force-impairment mechanism that is believed to be brought about by the metabolic by-products of the cross-bridge cycle itself (1). Additionally, the lower iEMG values generally observed at the failure point for longer vs. shorter trials raises the possibility that maximum levels of neuromuscular activation may be systematically reduced as the duration of all-out sprint trials is increased.

With a mechanistic explanation for the progressive impairment of musculoskeletal forces identified, we next investigate whether the duration-dependency of sprinting performance might somehow be linked to the mechanics of external force application.

From Performance Variability to a Force Model for Sprinting

From the outset of our own experimental efforts, we employed a design strategy of altering three independent variables in order to maximize the sprint performance variation observed. First, we recruited individuals with large differences in their sprint performance capabilities (5, 30, 35). Second, we administered all-out sprint trials across a broad range of durations from 2 to 300 seconds over which we knew *a priori* that performance levels would vary considerably (5, 6, 30, 33). Third, we compared performances across different modes of sprint locomotion (33). A representative sample of the performance variability observed is illustrated for two runners and two cyclists each in Figure 4A.

Our initial objective was to standardize the variation attributable to the first of our independent variables: individual performance differences. After compiling a sizeable data set for sprint running, we found that individual differences could be standardized using a simple, two-step process (6, 30, 33). Step one is quantifying the upper and lower intensity limits that bracket the range of sprinting performances for each individual: 1) the maximum burst sprint of 2 seconds or less (Spd_{burst} for running; P_{burst} for cycling) and 2) the minimum intensity that elicits the maximum rate of aerobic metabolism (Spd_{aer} for running; P_{aer} for cycling). The difference between these upper and lower limits represents the full range of non-aerobic and therefore non-sustainable speeds ($Spd_{burst} - Spd_{aer}$) or power outputs ($P_{burst} - P_{aer}$) possible for sprint efforts. Step two is standardizing sprinting speeds or power outputs by expressing the performance achieved as a fraction of the individual's non-sustainable speed or power reserve (for example, $Spd_{burst} = 1.0$, $Spd_{aer} = 0.0$, etc.; see Fig. 4B).

In comparative terms, the fraction of an individual's non-sustainable speed or power is the sprinting equivalent of expressing endurance exercise intensities as a fraction of an individual's maximum aerobic power, or $\dot{V}O_{2max}$. Because endurance efforts rely predominantly on aerobic or sustainable sources of metabolic power, relative intensities need only be referenced to one variable: the minimum intensity eliciting the maximum aerobic

power of the performer (6, 30). In contrast, sprinting efforts rely on both sustainable and non-sustainable sources of metabolic power, and therefore need to be referenced to two variables: both the burst and aerobic maximum of the performer. Here, our primary impetus for developing an index of relative sprint exercise intensities was the potential for predicting all-out sprint trial durations.

Our expression of relative sprinting intensities did, in fact, lead us to a direct means by which to quantify the variability introduced from our second independent variable: sprint trial duration. This is illustrated by the first two panels appearing in Figure 4. When the absolute sprinting performances in Figure 4A were expressed as fractions of the non-sustainable speed or power of the individual performers, their relative sprinting intensities fell in essentially the same duration-dependent manner within the respective modes (Fig. 4B). Thus, the relationship between trial duration and relative sprinting intensity can be described using single, mode-specific exponents (k_{run} or k_{cycle}) that provide the respective curves:

$$\text{Running: } \text{Spd}_{\text{FNS}}(t) = e^{(-k_{\text{run}} \cdot t)} \quad (\text{eq. 3})$$

$$\text{Cycling: } P_{\text{FNS}}(t) = e^{(-k_{\text{cycle}} \cdot t)} \quad (\text{eq. 4})$$

Where $\text{Spd}_{\text{FNS}}(t)$ and $P_{\text{FNS}}(t)$, respectively, represent the fraction of the non-sustainable speed and power that can be maintained for an all-out sprint trial of duration t , e is the base of the natural logarithm, and k_{run} and k_{cycle} are the exponents that describe the duration-dependent decrements in relative sprinting intensities within each mode of exercise. Validations of our model using hundreds of running trials administered to both sprint and endurance athletes, over a broad range of durations, and in both field and laboratory settings, have predicted the performances observed to within 2-4% on average (6, 30).

The performance variability introduced by the third variable, mode of exercise, was perhaps the most difficult to quantify as there is no standardized approach for equating absolute running speeds and cycling power outputs. Moreover, even after standardization of the different absolute speed and power output values to relative sprint intensities, large between-mode differences in the relative intensity-duration relationship were present (Fig. 4B). Relative sprint cycling performances fell more sharply in relation to trial duration than relative sprint running

performances did, as reflected in the two-fold difference in exponential values (33) providing the best empirical fits to the respective data ($k_{\text{run}} = 0.013 \text{ s}^{-1}$; $k_{\text{cycle}} = 0.026 \text{ s}^{-1}$).

We attribute this two-fold, between-mode difference to a corresponding difference in the fractional duration of external force application in the different modes of sprint exercise. Each pedal revolution involves consecutive periods of limb-pedal force application by the right and left legs that occur in virtually immediate succession. In contrast, consecutive periods of limb-ground force application during each running stride are separated by aerial periods of equivalent duration during which no ground force is applied (Fig. 2B+E). Accordingly, the fraction of the total sprint time that involves external force application by a single limb to the pedal or ground, i.e. the duty factor (DF), is two times greater for cycling than sprint running ($DF_{\text{run}} = 0.24$, $DF_{\text{cycle}} = 0.50$). When duration-dependent decrements in relative sprint cycling and running performance are expressed in terms of the time of external force application only (trial time \cdot DF), rather than the total sprinting time, decrements in the two modes conform to a common relationship (Fig. 4C).

This third model element quantitatively links the duration dependency of performance expressed in eqs 3 and 4, to the mechanics of external force application introduced originally in eqs 1 and 2. Given the limited variation of the length and frequency terms in eqs 1 and 2 previously noted, the performance-duration relationship predominantly reflects a duration-dependency in the maximal forces the musculoskeletal system can produce and apply externally (33). The existence of an apparently common relationship between relative sprinting intensities and the duration of external force application across two mechanically distinct modes of sprint exercise has several basic implications. First, at the whole-body level, that fraction of the sprint running speed or cycling power output provided by non-sustainable, anaerobic sources of chemical energy has a discrete duration dependency dictated by the cumulative duration of external force application. Second, the duration-dependency observed results from a rapid, progressive impairment of muscular force resulting from a reliance on anaerobic sources of chemical energy to fuel the contractions dictated by the mechanics the exercise requires. This demand-driven, fatigue-based explanation is fully consistent with numerous observations: the virtually immediate and progressive fatigue evidenced in our EMG data (5), rates of fatigue that are intensity dependent, the more rapid time course of fatigue in cycle vs. run trials of similar duration (Fig. 4B), and muscle force impairment at the cellular level resulting from the metabolic by-

products of a reliance on anaerobic metabolism to fuel the contractile activity supporting external force application (1, 5, 33).

Although aspects of our sprinting performance model remain a work in progress, our design strategies and force application framework have provided empirical, predictive and testable outcomes that have not come forth from the energy supply limit models. These include: quantification of relative sprinting intensities, identification of a common duration-dependency of relative sprinting performances, linking the duration-dependency of performance to external force application, and the identification of a force-impairment explanation for the duration-dependency of sprinting performance that can be tested at the tissue and cellular levels.

Metabolic Energy Release during Sprinting: Driven by Demand or Limited by Supply?

The tradition of conceptualizing all-out locomotor performance as a metabolic energy input, and therefore supply-limited endeavor originated nearly a century ago with the work of independent, contemporary scholars, A.V. Hill (10, 11) and Rodolfo Margaria (16-18). Hill related approximations of the metabolic energy available to record performance data from a variety of species and modes of human locomotion. Margaria and colleagues attempted to quantify the maximum rates of chemical energy release during all-out runs of different durations via direct experimentation. While both investigators provided the foundations for energy supply-limit modeling that continues to this day (Hill: 13, 14, 22, 27, 28; Margaria: 8, 9, 23), they reached opposite conclusions regarding sprint performance limitations. Margaria was sufficiently convinced of an energy supply limit, even for burst-type sprints as short as 2-3 seconds that he introduced the term “anaerobic muscular power” to describe them (16, 17). He further proposed that sprint performances measured in mechanical units should be expressed in metabolic terms (17). In contrast, in his original 1925 work on performance limits, Hill stated: “It is obvious that we cannot pursue our (metabolic energy supply) argument to times below about 50 seconds”, as these performances are limited by factors “mechanical and nervous” (10). Nonetheless, nearly a century after Hill published his conclusion, the supply-limit models he inspired continue to be applied (14, 22, 27, 28) to the very sprint performances that he recognized they could not explain.

The numerous energy supply-limit models that have come forth since Hill and Margaria differ in their specific features, but share a common characteristic: none has been empirically validated because the data required

to do so are not available. In the continued absence of valid whole-body anaerobic energy release measurements, these models have been formulated with largely uncertain and widely varying assumptions (2) regarding: the quantities of the anaerobic and aerobic energy available, their respective release rates, and the efficiency with which chemical energy is converted into speed, power, and force. Thus, the close fits that these models can provide to performance data are achieved by incorporating assumptions that have unknown or poor (28) validity as aptly noted (2, 27). Critical consideration of the explanations these models offer for sprinting performance is overdue, particularly given the performance-duration patterns that are now available for well-controlled sprint trials of very brief durations.

In their original view of burst and brief sprint exercise performance, Margaria and colleagues estimated that chemical energy re-supply to the contractile machinery could operate at maximal power for durations of 5-6 seconds (16, 17). Hence, these investigators also believed that maximal sprinting intensities could be maintained for durations of 5-6 s before further increments in duration and slowing rates of energy re-supply would compromise performance. Yet, the data now available demonstrate that performance decrements begin to follow a negative exponential pattern that occurs either instantaneously at the outset of exercise or within the first 2-3 s (5, 6, 33). Thus, in contrast to the “anaerobic” muscular power limitation proposed by Margaria, the greatest decrements in sprinting performance occur precisely over those very brief durations during which: 1) the rates of anaerobic energy re-supply to the contractile machinery are most rapid, and 2) intracellular stores of chemical energy are greatest.

A second difficulty with the energy supply limit models is mechanistic inconsistency with energetic measurements at the cellular level. One of the most widely noted features of muscle cell metabolism is the relative constancy of intracellular concentrations of the ATP molecule that serves as the immediate source of chemical energy to the contractile proteins. This well-regulated maintenance, even during the most intense contractile periods, is attributable to the rapid, one-step creatine phosphokinase reaction that re-supplies ATP. Accordingly, this near-equilibrium reaction is widely regarded as a temporal buffer that safeguards intracellular energy stores (15). Indeed, measurements made possible within living skeletal muscle by NMR spin technology indicate that the phosphocreatine reaction is capable of re-synthesizing ATP several times more rapidly than the contractile proteins within the muscle cells can use it (21). Thus, the rate-limiting step in the release of chemical energy at the cellular

level has been conclusively shown to be the contractile event that uses the energy and not the metabolic pathways that re-supply it.

Beyond the mechanistic inability to explain whole-body performance patterns and cellular-level energetic data during intense periods of contractile activity, energy supply-limit models also imply or predict that: 1) sprinting performance should be impaired when the total metabolic power available is reduced, and 2) sprinting performance should be largely unaffected by interventions that alter the mechanics of sprint exercise. Neither expectation has been borne out by the whole-body data that are now available. In the first case, hypoxic conditions have been used to reduce the availability of metabolic energy from aerobic metabolism during brief, all-out sprint efforts. In our running experiments (32), we found little difference between normoxic and hypoxic sprint performances lasting 60 s or less, despite aerobic contributions that were reduced by as much as 25% in the hypoxic condition. In the second case, mechanical interventions that prolong the lengths of external force application in accordance with our original, force-performance equations (eqs. 1 and 2) have consistently enhanced sprinting performance. These include: elliptical pedal orbits that increase single-leg cycling power outputs (20) by prolonging the down-stroke portion of the pedal stroke (eq. 2), artificially compliant, lightweight, double-lower limb prostheses that enhance running speeds (31) by prolonging contact lengths, reducing limb repositioning times and elevating stride frequencies (eq. 1), and hinged-blade ice skates that increase speed by prolonging the duration of the push-off portion of the skating stance phase (7).

Perhaps the most compelling evidence that energy release is demand-driven in accordance with mechanical requirements of sprint exercise rather than rate-limited by the supply of metabolic energy comes from our run-cycle comparisons (33). Specifically, if energy release during sprinting is in fact demand-driven, the absolute sprinting intensities and rates of energy release should both be greater in the mode of exercise during which force application and the supporting muscular contractions are relatively longer. Our run-cycle comparison is simplified by mechanics that involve largely the same limb extensor muscles for force application, and the similar maximal aerobic powers of the subjects tested in the respective modes (6, 33). When sprint cycling and running intensities are expressed as multiples of the respective aerobic maximums, the relative performances achieved are more than 50% greater during very brief cycling vs. running bouts (3.1X vs. 1.8X). When rough approximations of peak rates of metabolic energy release were made by extrapolating the linear metabolic rate-running speed, and metabolic rate-power output

relationships, that are measurable below $\dot{V}O_{2\max}$ to the intensities attained during sprinting, these estimates, like the factorial sprinting intensities achieved, were 1.5 times greater during very brief sprint cycling vs. running (Fig. 2C+F). Both results are consistent with energy release being driven by the mechanical demands of sprint exercise. Neither is consistent with the traditional view of a single whole-body limit on maximal anaerobic power that generalizes across modes of exercise (16-18).

Conclusions: Does Metabolic Power Matter for Sprinting?

The conclusion that sprinting is not energy supply-limited as traditionally conceived (8, 9, 14, 16-18, 22, 23, 27, 28) prompts the general question of the functional role metabolism does play and the specific question posed in our title: does metabolic power matter for sprinting performance? For burst-type sprints that last only a few seconds, a wealth of data spanning multiple levels of biological organization are fully consistent in indicating that the availability of metabolic power neither determines nor directly limits performance. These burst sprints predominantly reflect musculoskeletal function and not the “anaerobic muscular power” of Margaria (16, 17) or the many anaerobic fitness parameters that evolved subsequently. Nonetheless, metabolic power does assume progressively greater functional relevance as the duration of all-out sprinting extends from a few seconds to a few minutes, but in this case also, not in keeping with the traditional conceptualization. The predictive success of our force application model, both within and across modes, indicates that as efforts extend from a few seconds to a few minutes, the fractional reliance on anaerobic metabolism progressively impairs whole-body musculoskeletal performance, and does so with a rapid and remarkably consistent time course. In this respect, the sprint portion of the performance-duration curve predominantly represents, not a limit on the rates of energy re-supply, but the progressive impairment of skeletal muscle force production that results from a reliance on anaerobic metabolism to fuel intense, sequential contractions (Fig. 1).

Thus, the duration-dependence of the performances of elite human sprinters, cheetahs and other vertebrate animals that rely on skeletal muscle is attributable to the provision of chemical energy from both sustainable and non-sustainable sources in their natural engines. In contrast to synthetic engines that can convert chemical energy into force and mechanical power with relatively constant efficiency and without fatiguing, skeletal muscle has an

intrinsic duration-dependence directly linked to that proportion of the muscular force derived from the non-sustainable, anaerobic sources. From a design standpoint, these non-sustainable energy sources markedly enhance the range of musculoskeletal performances possible, but do so only transiently because the additional mechanical function provided is so rapidly compromised.

In closing, we offer three basic conclusions regarding sprint exercise performance and a biological contrast they reveal. First, the view that brief, all-out exercise performance is directly limited by rates of chemical energy provision to the contractile machinery in skeletal muscle is no longer supportable. Second, the metabolic energy released during sprinting is demand-driven and not supply-limited. Third, sprint exercise performance is determined by the application of musculoskeletal forces with a duration-dependency dictated by how rapidly these forces are compromised by rates of fatigue *in vivo*.

Finally, we note that the relationship between exercise mechanics, metabolism and performance differs fundamentally between sprint and endurance exercise. Although a common relationship has traditionally been assumed to generalize across a broad duration continuum of sprint and endurance efforts, contemporary evidence indicates otherwise. For endurance events, the metabolic energy available via sustainable, aerobic sources of metabolism predominantly determines performance by setting the intensity of the musculoskeletal mechanics that can be sustained throughout the effort. For sprint efforts, precisely the opposite is true: the intensity of the mechanical activity that the musculoskeletal system can transiently achieve determines the quantities of metabolic energy released and the level of performance attained.

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Figure Captions

Figure 1. A schematic representation of the non-sustainable force application model of sprinting performance. The horizontal lines identify the upper (dashed, mechanical) and lower (solid, aerobic) bounds of the range of sprinting, or non-sustainable performances for whole-body sprint exercise. Performance (e.g. running speed or cycling power output) levels fall in a characteristic fashion as the duration of the sprint event becomes more prolonged.

Figure 2. The direct relationship typically observed between the external force applied and level of performance attained for cycling (A; data from 33) and running (D; data from 6, 35). Consecutive periods of force application by opposite limbs occur in immediate succession during cycling (B; adapted from Seargent *et al.* ref. 25) but are separated by aerial periods without force application during running (E; data from 34). Hypothesized rates of chemical energy utilization by the contractile elements of the extensor muscles activated during sprint cycling (C) and running (F) are schematically presented as square waves for simplicity. [Notes: The horizontal bars above the force waveforms in B and E identify the durations of pedal revolutions or stride times and the periods of external force application.] The ground and pedal forces illustrated correspond to the F_g and F_{ds} terms in equations 1 and 2, respectively.

Figure 3. Representative data from numerous cycling trials (A, B) and a single sprint running trial (C, D). Integrated EMG data from the muscle contractions occurring in the non-fatigued state at the outset of each cycling trial are directly related to the pedal forces applied (A). Ground (C) and pedal forces (not shown) did not vary over the course of individual sprint running and cycling trials. In contrast, the EMG activity of the limb extensor muscles activated to support external force application increased continuously throughout each sprint trial (B, D) to maintain the constant force required. Data acquired as in reference #5 and 34.

Figure 4. Decrements in all-out cycling power output and running speed for two individual subjects (A), during cycling (33) and running (6). When the individual sprint performances in A were expressed as relative sprinting intensities (i.e. fraction of the subject's non-sustainable speed or power reserve), duration-dependent decrements in

cycling performance were twice as large for cycling vs. running (B). When the same relative sprint cycling and running performances are expressed in terms of the time of external force application only (trial time • duty factor; $DF_{run} = 0.24$, $DF_{cycle} = 0.50$), rather than the total sprinting time, as in B, the duration-dependency of relative sprinting performance in the two modes of exercise becomes essentially identical (C).

Fig 1

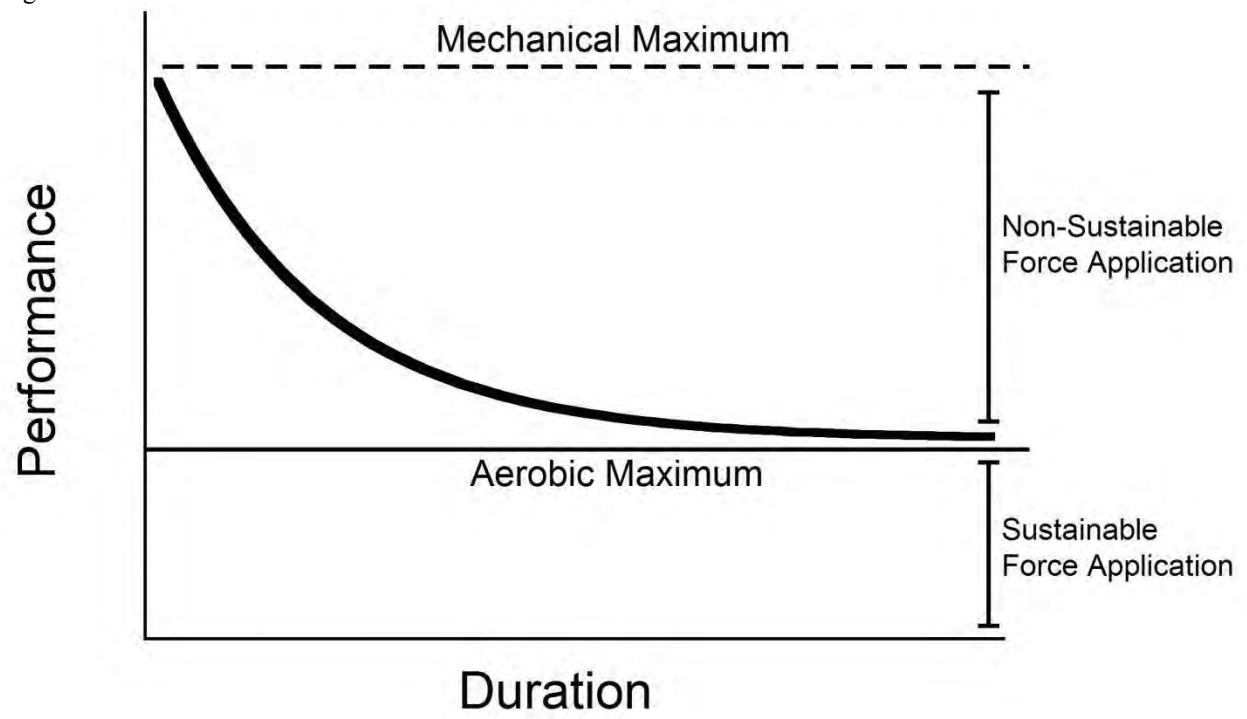


Fig 2

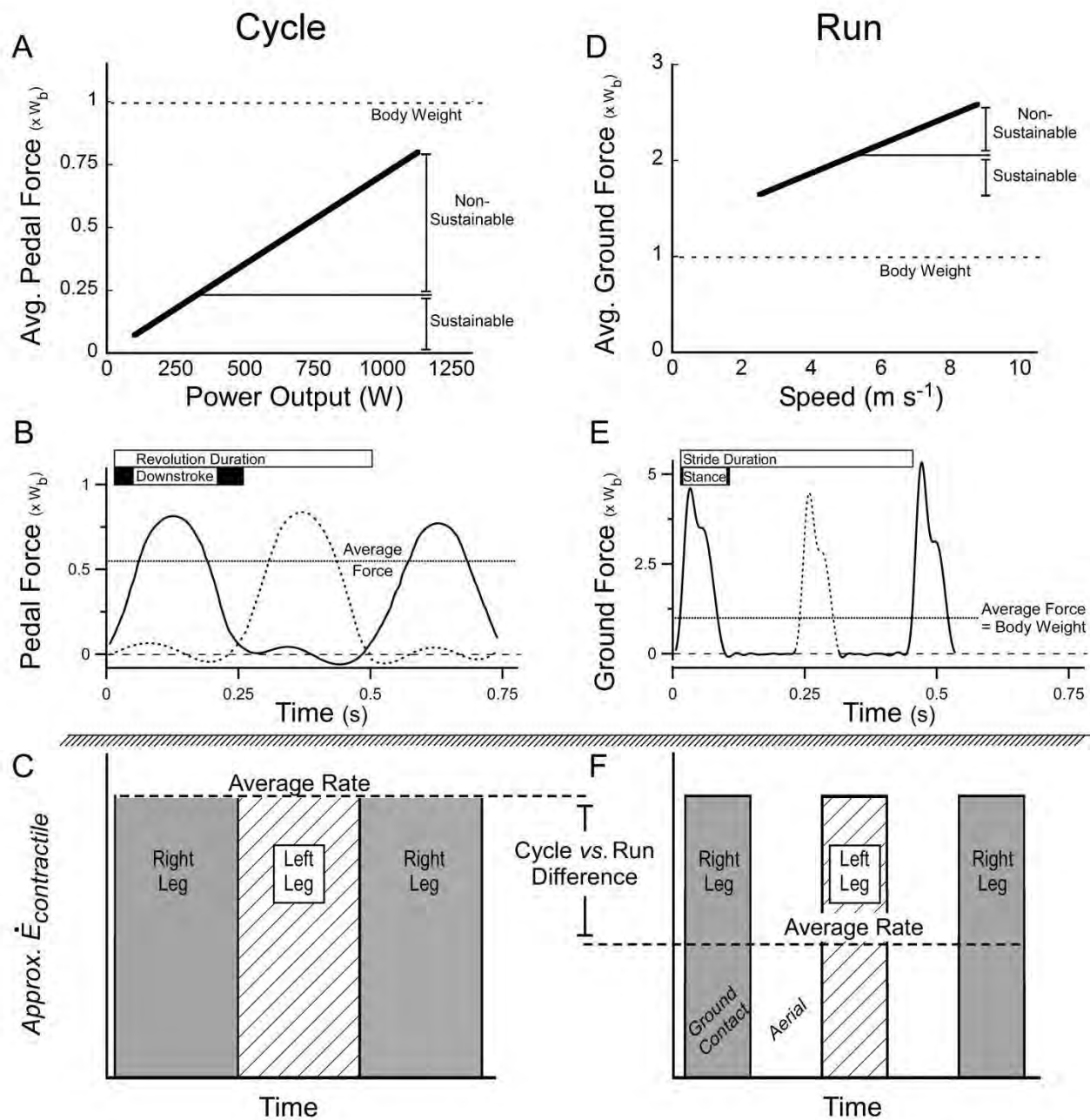
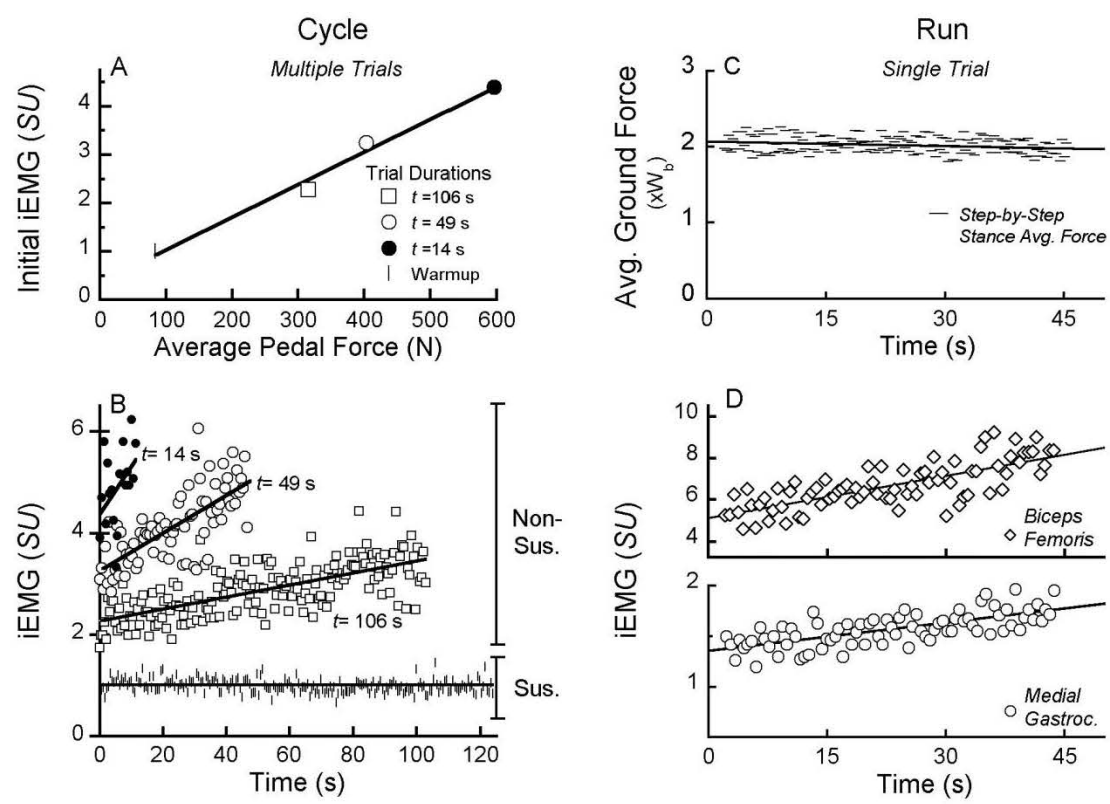
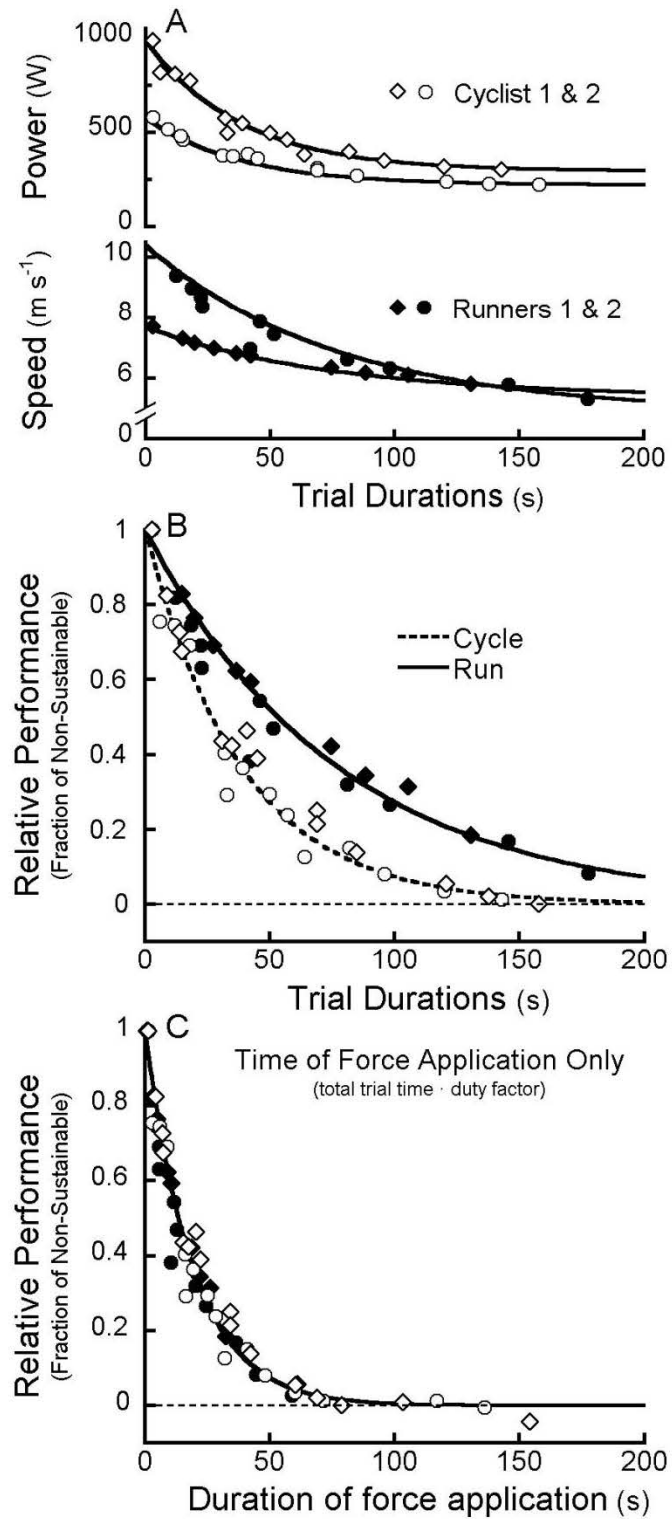


Fig 3





The mass-specific energy cost of human walking is set by stature

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SUMMARY

The metabolic and mechanical requirements of walking are considered to be of fundamental importance to the health, physiological function and even the evolution of modern humans. Although walking energy expenditure and gait mechanics are clearly linked, a direct quantitative relationship has not emerged in more than a full century of formal investigation. Here, on the basis of previous observations that children and smaller adult walkers expend more energy on a per kg basis than larger ones do, and the theory of dynamic similarity, we hypothesized that body length (or stature, L_b) explains the apparent body size-dependency of human walking economy. We measured metabolic rates and gait mechanics at six speeds from 0.4 to 1.9 $\text{m}\cdot\text{s}^{-1}$ in 48 human subjects who varied by a factor of one and one-half in stature, and approximately six in both age and body mass. In accordance with theoretical expectation, we found the most economical walking speeds measured ($\text{J}\cdot\text{kg}^{-1}\cdot\text{m}^{-1}$) to be dynamically equivalent (i.e. similar U ; where $U = \text{velocity}^2/\text{gravity} \cdot L_{\text{leg}}$) among smaller and larger individuals. At these speeds, stride lengths were directly proportional to stature while the metabolic cost per stride was largely invariant ($2.74 \pm 0.12 \text{ J}\cdot\text{kg}^{-1}\cdot\text{stride}^{-1}$). The tight coupling of stature, gait mechanics and metabolic energy expenditure resulted in an inverse relationship between stature and mass-specific transport costs ($\text{J}\cdot\text{kg}^{-1}\cdot\text{m}^{-1}$; $E_{\text{trans}}/M_b \propto L_b^{-0.95}$). We conclude that humans spanning a broad range of ages, statures and masses incur the same mass-specific metabolic cost to walk a horizontal distance equal to their stature.

INTRODUCTION

The metabolic and mechanical requirements of human walking influence a broad array of structural, functional and health relationships. This global functional importance has stimulated a body of scientific literature that now spans more than a century and encompasses a variety of experimental objectives. These range from basic biological inquiry to applied efforts to predict speed, energy expenditure and other variables in laboratory and field settings. However, in spite of the extensive scientific consideration human walking has received, some aspects of basic understanding remain limited.

A primary example of incomplete contemporary understanding is the body size dependency long observed for the metabolic requirements of this gait. As would be expected, larger individuals do expend more energy than smaller ones when the metabolic energy expended is expressed in absolute terms. However, the differences observed are not directly proportional to body mass. When expressed on a per kg basis, the energy expended to walk a fixed distance or at a given speed can be as much as two to three times greater for smaller vs. larger individuals. At present, a quantitative explanation for the relationship between body size and the energy cost of human walking has not been established.

The greater mass-specific metabolic rates consistently observed for smaller vs. larger human walkers have been considered from several perspectives. Ontogenetic approaches have appropriately considered both maturation (DeJaeger et al., 2001; Morgan et al., 2002) and body size (McCann and Adams, 2002), but have not resolved their quantitative importance. Mechanical approaches have estimated that the mass-specific mechanical work that small children and adults perform during walking differs only marginally (Cavagna et al., 1983; Bastien et al., 2003; Schepens et al., 2004), and therefore cannot account (Schepens et al., 2004) for the much larger differences observed in metabolic cost. The current lack of quantitative understanding is reflected in the use of different generalized equations to estimate the energy expended by adult (ACSM, 2006; Pandolf et al., 1971) and child populations (Morgan et al., 2002). In both cases, population-specific equations predict the same mass-specific metabolic rates for individuals who differ in height and weight.

A potential explanation for the apparent body-size dependency of the metabolic cost of human walking is a corresponding rate dependency in executing the mechanics of each walking stride (Alexander, 1976; Heglund and Taylor, 1988). Clearly, the shorter statures of smaller vs. larger walkers require more, and more frequent, strides in order to travel any fixed distance, or at any given speed. If the mechanical components of each walking stride were to require the same expenditure of metabolic energy per kilogram of body mass, shorter walkers might have greater mass-specific metabolic rates simply because they take more frequent strides. This possibility seems most plausible if shorter and taller individuals were to walk in dynamically similar ways, i.e. with both stride lengths and times related to the body's length (L_b) by some constant proportion. Although widely embraced (DeJaeger et al., 2001; McCann and Adams, 2002; Cavagna et al., 1983), the validity of the dynamic similarity assumption is not strictly known. Thus, the simple possibility that the energy cost per stride at equivalent speeds may be the same for short and tall individuals has not been evaluated.

Here, we tested the idea that the mass-specific energy cost of human walking is determined by stature. Our expectations of approximate geometric similarity in bodily proportions and dynamic similarity in gait among shorter and taller individuals led us to evaluate this idea in two ways. First, we hypothesized that the mass-specific metabolic energy expended per stride would not vary between short and tall individuals. Second, we hypothesized that mass-specific energy expended per unit distance walked would be inversely related to stature ($\propto L_b^{-1.0}$). Both hypotheses were tested at equivalent walking speeds.

MATERIALS AND METHODS

Experimental design

We employed several design strategies to maximize the rigor of the two tests of our stature hypothesis. First, we recruited subjects who spanned relatively broad ranges of age, stature, and body mass. Second, we divided the 48 subjects recruited into four discrete groups on the basis of stature to minimize the influence of individual variability in walking economy that is not related to stature on our analyses. Third, we significantly increased the robustness of our scaling analysis by using the published literature to expand the number of stature groups included from our original four groups to a total of 29. Fourth, we took considerable care to address two issues that could potentially confound both hypothesis tests: 1) making metabolic comparisons only at those walking speeds that are equivalent for subjects of different statures, and 2) correctly partitioning basal vs. walking metabolism.

Equivalent Walking Speeds: Because walking transport costs vary with speed and do so in a stature-dependent fashion (DeJaeger et al., 2001; McCann and Adams, 2002), identifying equivalently economical speeds for individuals of different body sizes was a critical prerequisite for valid analysis. Intuition and previous results (DeJaeger et al., 2001; McCann and Adams, 2002; Alexander, 1976) both indicated that any given absolute speed would be relatively slower for shorter individuals and relatively faster for taller ones. Accordingly, the speeds of our subjects were not likely to be either equivalent (Alexander, 1976), or equivalently economical (Heglund & Taylor, 1988) at any given absolute speed. We adopted an empirical solution to this challenge, identifying equivalent speeds for shorter and taller individuals as that speed at which a minimum transport cost ($E_{\text{trans-min}}$, $\text{J}\cdot\text{kg}^{-1}\cdot\text{m}^{-1}$) was measured for each. These empirically determined minimums were subsequently used to compare the energy cost per walking stride and to identify the exponential relationship of best-fit between metabolic transport costs and stature.

Given the critical importance of making stature-based comparisons at walking speeds that are equivalent, and equivalently economical, for smaller and larger individuals, we adopted two post-hoc criteria to evaluate whether the most economical walking speeds were mechanically equivalent: the duty factor, or ratio of foot-ground contact time to total stride time (t_c/t_{str}) and the Froude number derived from the principle of dynamic similarity (i.e. similar U ; where $U = \text{velocity}^2/\text{gravity} \cdot L_{\text{leg}}$). In the event that the most economical speeds measured for the different stature groups were not equivalent, these two well-established mechanical indices would quantify the lack of equivalence present. Alternatively, the equivalence expected would result in the most economical speeds observed increasing as

a predictable function of body length (speed at $E_{\text{trans-min}} \propto L_b^{0.50}$), but occurring at the same duty factor and Froude number in all four stature groups.

Basal vs. Walking Metabolism: Correctly quantifying the metabolic energy incurred by walking necessitated subtracting out that portion of the body's total metabolic rate devoted to non-walking, or basal metabolism. Although some investigators have subtracted the metabolic rate measured during quiet standing for this purpose, we subtracted basal, rather than standing metabolic rates. We did so because standing rates include muscular support costs (Joseph and Nightingale, 1952; Loram et al., 2007; Weyand et al., 2009) that are also incurred during walking (Biewener et al., 2004; DeJaeger et al., 2001; Grabowski et al., 2005; Griffin et al., 2003; McCann and Adams, 2002; Weyand et al., 2009). The basal rates subtracted from both our original data and qualifying literature data were calculated from the age, gender, mass and stature of each subject using the generalized equations of Schofield et al., (Schofield et al., 1985). Using estimates, rather than direct measures, was necessary in order to: 1) include the 25 qualifying group means from the literature in our scaling analysis, and 2) to treat both original and literature data points in the same quantitative manner. Directly measuring the basal metabolic rates of the subjects in the qualifying literature populations was clearly not possible. Accordingly, to also evaluate the predictive accuracy of the Schofield et al., equation estimates, we measured post-absorptive resting metabolic rates in six adult subjects who were available for testing, three male and three female.

The error introduced into our analyses of group data as a result of necessarily using estimated rather than measured basal metabolic rates was considered using both original measures and previously reported results. The Schofield et al., age, height, weight and gender equations have been extensively validated and are the most extensively used for this purpose. The error that results from using these equations to predict the mean basal metabolic rates of either children or adult groups was established in the original work as $\pm 2.2\text{-}3.4\%$ for groups of ten subjects (Schofield et al., 1985). Similar accuracy for predicting group means has been subsequently reported by a number of other investigators (De Loreonzo et al., 2001; Piers et al., 1997; Johnstone et al., 2006; Rodriguez et al., 2000; van der Ploeg et al., 2001).

Subjects

Forty-eight healthy individuals, 24 males and 24 females, between the ages of five and 32 years of age were included in the study. The 32 subjects who were 18 years of age or younger were tested at the Children's Nutrition Research Center of the Baylor College of Medicine while the 16 subjects who were over the age of 18 were tested at the Locomotion Laboratory of Rice University. Written informed assent and consent was obtained in accordance with the Institutional Review Boards of Baylor College of Medicine and Rice University. For the purpose of analysis and without regard to age, subjects were divided into four groups of the basis of stature (A, B, C, D). The age, gender, body mass (M_b), stature (L_b) and leg length (L_{leg}) means of the four stature groups appear in Table 1.

Treadmill Testing Protocol

Walking trials were administered on a level treadmill at constant speeds of 0.4, 0.7, 1.0, 1.3, 1.6, and 1.9 m•s⁻¹. The protocol began at 0.7 m•s⁻¹ and was administered continuously in a staggered speed fashion until all the speeds at which the subjects could maintain a walking gait were completed. After a first completion of the protocol, subjects were allowed a five to 10-minute break before repeating each walking speed a second time. The initial trial of each protocol lasted four to six minutes. Subsequent trials lasted until a minimum two-minute, steady-state period with respect to the rate of oxygen uptake was observed in real time. All the adult subjects tested walked steadily and provided reproducible rates of oxygen uptake at each speed. Four of a total of thirty-six children tested did not maintain a consistent position on the treadmill and had rates of oxygen uptake that differed by more than 5% across the different trials completed at common speeds. The data from these four children were not included in the analysis.

All subjects were instructed to walk and not run during the testing. The shortest subjects, those in group A, were able to walk at the four speeds through 1.3 m•s⁻¹ successfully, but could not attain speeds of 1.6 and 1.9 m•s⁻¹ without running. The subjects in group B were able to walk at the five speeds through 1.6 m•s⁻¹ successfully, but could not do so at 1.9 m•s⁻¹. All but three of the subjects in group C, and all the subjects in group D were able to walk at all six speeds including 1.9 m•s⁻¹.

Metabolic Measures

Indirect calorimetry was used to determine rates of metabolic energy expenditure from measurements of expired gases during steady-state treadmill walking using a computerized metabolic system (Parvo Medics TrueOne 2400, Sandy, Utah) per our previous description (Weyand et al., 2006). Expired gases were directed via a one-way breathing valve and corrugated tubing through a pneumotach into a mixing chamber. Aliquots were drawn from the mixing chamber and analyzed for O₂ and CO₂ fractions using paramagnetic and infrared gas analyzers, respectively. Rates of oxygen uptake at each treadmill walking speed were averaged over a two-minute steady-state period to obtain values for each trial. Measures from the two trials completed at each speed were averaged for subsequent analysis. Mean rates of oxygen uptake were divided by body mass and converted to rates of energy expenditure (E_{metab} , W•kg⁻¹) using an energetic equivalent of 20.1 joules per ml of O₂. The same Parvo Medics TrueOne metabolic system was used in both laboratory locations. The system was calibrated using a three-liter syringe to introduce volume flow rates that spanned the range of ventilation rates present during testing. The O₂ and CO₂ analyzers were calibrated using a two-point calibration procedure using room air and known concentrations in the physiological range for expired gases. Validations of the TrueOne system were performed using precision blended N₂-CO₂ mixtures infused at rates to simulate rates of oxygen uptake ranging from 0.3 to 1.0 l•min⁻¹ in accordance with the technique described by Moon et al., (Moon et al., 1995). The agreement between precision-simulated rates of oxygen uptake and those measured by the TrueOne metabolic system across 15 infusion trials spanning the aforementioned range was $2.8 \pm 2.0\%$.

Gross, mass-specific, metabolic rates (W•kg⁻¹) were converted to net, mass-specific metabolic rates (W•kg⁻¹) by subtracting rates of basal metabolism in accordance with the original suggestion of Schmidt-Nielsen (Schmidt-Nielsen, 1972). The basal rates subtracted for individual subjects were estimated from the generalized equations of

Schofield et al., (Schofield et al., 1985) using age, height, weight and gender. Resting metabolic rates were also measured in six adult subjects who lay quietly in a supine position for a minimum of 60 minutes after reporting to the laboratory in a post-absorptive state in the early morning. Resting metabolic rate was determined from the lowest consecutive ten-minute average over the last 30 minutes of testing. The mean value from this group of six subjects was compared to that predicted by Schofield et al., to directly assess the predictive accuracy of the Schofield equations on a portion of our original data.

Metabolic or walking transport costs, i.e. the mass-specific, metabolic energy expended to walk a unit distance (E_{trans} , $\text{J}\cdot\text{kg}^{-1}\cdot\text{m}^{-1}$) were determined by dividing net, mass-specific metabolic rates by the speed of the walking trial. Additionally, walking transport costs were standardized to body length by dividing net, mass-specific transport costs by stature to obtain the net, mass-specific metabolic energy expended to travel a distance equal to the height of the body ($\text{J}\cdot\text{kg}^{-1}$).

Walking kinematics

The durations of each stride and foot-ground contact period were determined from 30 Hz video (Sony model DCR-TRV19; 30 Hz) by counting the frames during slow playback over 25 consecutive contact periods of the same foot. Stride time (t_{str}) was defined as the time elapsing between consecutive foot strikes of the same foot. Stride length (L_{str}) was determined by multiplying stride time by belt speed. Foot-ground contact time (t_c) was determined from the number of frames a single foot was in contact with the treadmill belt. Duty factor was determined by dividing foot-ground contact time by stride time (t_c / t_{str}). An index of equivalent speed (U) was determined from walking speed (V), leg length (L_{leg}) and gravity (g) using the Froude number: $U = V^2 \cdot g^{-1} \cdot L_{\text{leg}}^{-1}$. Leg lengths were measured by palpating the hip joint axis of rotation during standing and slow swinging of the limb in the sagittal plane. One subject (stature - 1.77 m) in group D was not available for leg length measurements after completing the metabolic testing.

The scaling of walking transport costs with body size

Best-fit exponential relationships between the minimum measured metabolic cost of transport ($E_{\text{trans-min}}$) and both stature and body mass were conducted on both our original stature group means and on these original data plus qualifying group means taken from the literature. Literature values were included only from those studies that provided the information necessary to conduct the same analysis as that performed on our original data: stature, body mass and steady-state gross metabolic rates during level walking across a sufficient number of speeds to exhibit a minimum. A data point was considered a valid minimum only when greater values from both faster and slower speeds were also reported. Our literature search of more than 115 original potentially qualifying studies dating from the early 1900's forward yielded 25 group means that satisfied these criteria. We did not include data points from subjects ≥ 65 years of age, because they may not walk in a dynamically similar manner to individuals who are less than 65 years old (Ortega and Farley, 2007). Qualifying literature data and sources are reported in Table 2.

In addition to predicting a stature scaling exponent of -1.0 for human walking economy, our theoretical framework can also be used to predict a scaling exponent for body mass. Among geometrically similar subjects, body mass (M_b) increases with stature to the third power ($M_b \propto L_b^{3.0}$). Therefore, given the approximate geometric similarity we assumed *a priori* for our test subjects, our stature hypothesis ($E_{\text{trans-min}} \propto L_b^{-1.0}$) predicts that the mass-specific energy cost of human walking should scale with body mass to the negative one-third power ($E_{\text{trans-min}} \propto M_b^{-0.33}$).

Statistics

Group means for physical characteristics (body mass, stature, leg length) as well as the metabolic energy expended per stride ($\text{J} \cdot \text{str}^{-1}$), and mechanical data (stride length, duty factor, Froude number) at the most economical walking speed were assessed using a one-way ANOVA with a Tukey test of post-hoc means. Gender differences in net metabolic rates were assessed using unpaired t-tests within each of the height groups in order to control for the effect of stature. Percentage error was determined as: $((\text{predicted} - \text{actual}) / \text{actual}) \times 100$.

RESULTS

Walking energy expenditure

The gross, mass-specific metabolic rates measured at six walking speeds from 0.4 to 1.9 m•s⁻¹ conformed to patterns expected on the basis of stature. These rates increased in a curvilinear fashion with walking speed for all four stature groups (Fig. 1A), roughly doubling from the slowest to the fastest walking speed within each group. Group means ranged from an overall minimum of $2.56 \pm 0.06 \text{ W} \cdot \text{kg}^{-1}$ to a maximum of $6.80 \pm 0.14 \text{ W} \cdot \text{kg}^{-1}$. At each of the six speeds, and for all 28 of the between-group comparisons possible, gross, mass-specific, metabolic rates varied in an inverse manner with stature, differing by a factor of one and one-half to two between the shortest and tallest groups.

For all four stature groups, walking transport cost-speed relationships conformed to the same general pattern, exhibiting minimums at intermediate walking speeds, and greater values at both slower and faster ones (Fig. 1B). Like gross metabolic rates, net walking transport costs were inversely related to stature, with the minimums of the four stature groups varying by a factor of just less than one and one-half between the shortest and tallest group [Group A: $3.07 \pm 0.14 \text{ J} \cdot \text{kg}^{-1} \cdot \text{m}^{-1}$; Group D: $2.12 \pm 0.17 \text{ J} \cdot \text{kg}^{-1} \cdot \text{m}^{-1}$]. Within stature groups, walking transport costs were not related to gender.

Walking transport costs standardized to stature, which represent the net, mass-specific metabolic cost of transporting one kilogram a horizontal distance equal to the body's stature appear in Fig. 1C. This expression largely eliminated the between-stature group differences that were present prior to standardization for stature. At the four intermediate and most economical speeds from 0.7 through 1.6 m•s⁻¹, the overall mean value for the net metabolic energy required to travel a forward distance equal to the body's stature was 3.93 Joules per kilogram ($0.94 \text{ calories} \cdot \text{kg}^{-1}$).

The mass-specific metabolic energy expended per stride at most economical walking speeds did not differ among the four stature groups (Table 3), and varied by an average of only 4.4% for the six between-group comparisons possible.

Basal energy expenditure

The mean basal metabolic rates for stature groups A, B, C, and D, as calculated from the Schofield et al., equations were: 2.18 ± 0.12 , 1.55 ± 0.06 , 1.31 ± 0.04 , and $1.13 \pm 0.03 \text{ W} \cdot \text{kg}^{-1}$, respectively. These values comprised 43.0, 38.0, 34.8 and 30.9% of the gross metabolic rates measured for the respective groups at their most economical walking speeds. The mean basal metabolic rate values calculated using the Schofield equations for all 25 literature group values included in the scaling analysis, and their fractional contributions to the total metabolic rates reported during walking appear in Table S1.

The average percentage difference between the mean metabolic rates predicted by the Schofield equations and the actual post-absorptive resting rates measured in the six original adult subjects tested was $+3.2 \pm 1.4\%$ [1.11 ± 0.02 vs. $1.08 \pm 0.02 \text{ W} \cdot \text{kg}^{-1}$, respectively].

Scaling of the energy cost of human walking

The exponents providing the best fit between walking transport cost minimums and stature ($E_{\text{trans}} \propto L_b^{-0.90}$) and mass ($E_{\text{trans}} \propto M_b^{-0.32}$), respectively, among our original four stature groups were in good agreement with our theoretical predictions ($E_{\text{trans}} \propto L_b^{-1.0}$ and $M_b^{-0.33}$, respectively; Fig. 2A and B). When literature values with the necessary information: stature, body mass, and gross metabolic rates across a sufficient number of speeds to exhibit a clear minimum, were added to the analysis, the exponential scaling factors for stature ($E_{\text{trans}} \propto L_b^{-0.95}$) and body mass ($E_{\text{trans}} \propto M_b^{-0.29}$) were both within 0.05 or less of the values predicted.

The relationship that best described the stature to mass relationship for our four stature groups conformed reasonably to our expectation of geometric similarity: $M_b = 15.2 \cdot L_b^{2.83}$, where mass is measured in kg and stature in meters.

Mechanical equivalency of the most economical walking speeds

The stature group means for the most economical walking speed, stride length to body length ratios (L_{str}/L_b), duty factors (t_c/t_{str}), and Froude numbers, respectively, appear in Table 3. The most economical walking speeds of the respective groups increased with the linear dimensions of the body as expected (speed at $E_{\text{trans-min}} \propto L_b^{0.52}$), and the ratio of stride length to body length, the duty factor and the Froude number were all essentially identical across the four different stature groups at their respective most economical walking speeds.

DISCUSSION

We set out to evaluate the straightforward hypothesis that the mass-specific energy cost of human walking is set by stature. Under the equivalent conditions necessary for valid comparisons, both of the empirical tests we conducted supported the validity of this basic idea. In accordance with our first hypothesis, we found that the mass-specific energy expended per walking stride was nearly invariant among subjects who varied by a factor of more than one and one-half in stature and roughly six in both age and body mass. This direct coupling of the stride cycle to the metabolic energy expended provides a single, simple explanation for the height, weight and age trends previously observed for the economy of human walking. Next, because the stride lengths of these subjects were directly proportional to their heights, we found the mass-specific energy expended per unit distance traveled was inversely related to stature. In the latter case, the exponents that best described the walking transport cost-stature relationship in our original (0.90), and original plus literature data (0.95) agreed well with the theoretical projection of our second hypothesis ($E_{\text{trans-min}} \propto L_b^{-1.0}$). Accordingly, we conclude that humans spanning a broad range of ages, statures and masses incur the same mass-specific metabolic cost to walk a horizontal distance equal to their stature.

Equivalent speeds and energy expenditure in walking gaits

A first issue of significant concern from the outset of the study was identifying speeds that were truly equivalent for individuals who spanned the broad range of body sizes examined. From the design stage forward, we recognized that the speed-specific nature of walking metabolic rates and transport costs, and the systematic variation of this speed-specificity in relation to stature would confound metabolic comparisons made at the same absolute speeds. We addressed this issue experimentally by making comparisons only at the most economical speeds measured for each of our respective stature groups. However, we could not know *a priori* exactly how well this experimental approach would ultimately identify the equivalent speeds desired.

Our *post-hoc* evaluations indicate that our empirical technique fully met the objective intended. First, as expected from both intuition and mechanical principles, the walking speeds that were most economical became progressively faster from the shortest to the tallest stature group. This stature-induced variability is well illustrated by the transport cost data of each of our four stature groups that appears in Figure 1B. The agreement between the increases in speed predicted from mechanical principles in relation to body and leg lengths (speed at $E_{\text{trans-min}} \propto L^{0.50}$) with the empirical values observed ($\propto L_b^{0.52}$; $\propto L_{\text{leg}}^{0.46}$) was nearly exact. In addition to supporting the efficacy of the empirical approach taken, this result also supports the general validity of our original assumptions regarding dynamic similarity in gait and approximate geometric similarity in bodily proportions among the subjects tested. Additional and equally robust empirical support for mechanical equivalence was provided by the two indices specifically used for this purpose: the duty factor and Froude number. As can be seen in Table 3, the duty factors and Froude numbers at the most economical speeds measured were all but identical across the four stature groups. Stride length to body length mean values were also virtually constant. The nearly exact agreement between theoretical mechanical predictions and empirical metabolic results provides compelling evidence that the body's

linear dimensions set both the gait and mass-specific metabolic cost patterns observed across individuals who differ in body size.

The second design concern was correctly subtracting basal contributions to gross walking metabolic rates. We used predictive equations, rather than direct measurements for this purpose because doing so was necessary for the inclusion and consistent treatment of the 25 qualifying literature group data points used in our scaling analysis. The literature amply supports the ability of the population equations used to predict group means (De Loreonzo et al., 2001; Piers *et al.*, 1997; Johnstone et al., 2006; Rodriguez et al., 2000; Schofield et al., 1985; van der Ploeg et al., 2001), indicating an approximate accuracy of three percent for the group sizes assessed here. Indeed, on the six adult subjects on whom we took direct measurements, this was the accuracy observed; the mean predicted value was 3.2% greater than the measured value. In specific application, the presence of a +3.2% error in the basal metabolic rate estimates of groups A, B, C, and D would underestimate the net metabolic rates quantified for walking by only 1.4 to 2.2%. These error values incorporate basal contributions to gross metabolic rates that averaged just over one-third for these four groups (mean = 36.7%; Results and Table S1). Thus, for our purpose of analyzing group data across a range of body sizes, empirical observations indicate that the technique utilized introduced negligible error while allowing for a consistent and considerably more comprehensive scaling analysis.

Hypothesis Test I: Equal mass-specific energy costs per stride?

Our first evaluation of a basic mechanistic link between stature and metabolic energy cost was a comparison of the net metabolic energy expended per stride at the most economical speeds for different-sized individuals. As can be seen in Table 3, the mass-specific metabolic energy expended on a per stride basis was essentially invariant across our four stature groups while stride lengths were directly proportional to stature. Because shorter and taller subjects do indeed walk in a dynamically similar fashion (Table 3), these data support the original idea that the metabolic energy expended to execute each walking stride at equivalent speeds is the same regardless of the stature of the individual. The direct coupling of stride and metabolic rates identifies the rates at which the movements of each stride are completed as a critical determinant of mass-specific metabolic rates. In contrast, existing literature amply indicates that the size-dependent economy of human walking cannot be explained by existing measures of the rates at which mechanical work is performed (Cavagna et al., 1983; Bastien et al., 2003; Schepens et al., 2004; Donelan et al., 2002; Kuo et al., 2005).

In the interest of providing a simple, quantitative expression of the direct link between walking mechanics and energy expenditure, we averaged the mass-specific energy expended per standardized unit distance at, and slightly beyond, the most economical walking speeds used for both of our hypothesis tests. For this additional purpose, we used the four speeds from our protocol that fall within the range of speeds that humans typically select during overground walking (Cavagna et al., 1983; Bornstein and Bornstein, 1976). At the four qualifying speeds from 0.7 to 1.6 m·s⁻¹, the mean energy expended by all four stature groups to travel a forward distance equal to their stature was 0.94 calories per kg. For simple application and more convenient cost estimation for individual walkers,

we rounded this mean to the more practical value of 1.0 calorie per kg and found that it provides a reasonable approximation (mean % error = 9.3%; n = 183 trials from 48 subjects) of the net, mass-specific metabolic cost of human walking on firm, level surfaces.

Hypothesis Test II: Are mass-specific transport costs inversely related to stature?

The results of our second hypothesis test: the scaling analysis conducted on our original four stature groups, also supported the basic validity of our original stature idea. The exponents providing the best fit between walking transport cost minimums and both stature ($E_{\text{trans-min}} \propto L_b^{-0.90}$) and mass ($E_{\text{trans-min}} \propto M_b^{-0.32}$), respectively, were in good agreement with our theoretical predictions ($E_{\text{trans-min}} \propto L_b^{-1.0}$ and $M_b^{-0.33}$, respectively; Fig. 2A and B). In the latter case, the mass exponent derived agreed with the classical value of Taylor et al., for adult birds and mammals to the second decimal place. When we tested the relationship more robustly, by adding literature values with the necessary information: stature, body mass, and gross metabolic rates across a sufficient number of speeds to exhibit a clear minimum, the exponents obtained agreed as well, or perhaps slightly better, with our original predictions. As can be seen in Fig. 2A and B, adding qualifying literature data (Table 2) to our original data yielded exponential scaling factors for stature ($E_{\text{trans}} \propto L_b^{-0.95}$) and body mass ($E_{\text{trans}} \propto M_b^{-0.29}$) that were both within 0.05 or less of the values predicted by our stature hypothesis.

General implications of both hypothesis tests

In addition to providing basic support for our stature hypothesis, the human data presented here and elsewhere can also be used to better evaluate the possibility that body mass (Nudds et al, 2009), rather than stature may provide a more direct explanation for the scaling of locomotor economy with body size. Several independent literature observations on humans support the opposite conclusion: that mass-specific transport costs are set by the length of the body and are minimally affected by variation in body mass at any given stature. First, obese and non-obese subjects of the same stature walk with similar mechanics (Browning and Kram, 2005; Browning and Kram, 2006) and have the same or very similar mass-specific metabolic costs (Browning and Kram, 2005; Browning and Kram, 2006; Ayub and Bar-Or, 2003). Second, subjects who lose weight have the same mass-specific, walking metabolic rates when body mass changes and stature does not (Hunter et al., 2008). Finally, a mechanistic basis for a causal link between mass-specific metabolic transport costs and body mass is difficult to envision whereas stature has a direct and highly predictable influence on the mechanics of walking (Table 3) that determine the muscular activity and costs incurred.

An additional conclusion that can be drawn from the direct relationship we have identified between stature and human walking economy is that ontogeny has no measurable effect on the metabolic cost of human walking that is independent of body size. Certainly inferior skill, coordination or perhaps mismatches between periods of muscular force development and muscle fiber speeds could all conceivably compromise the locomotor economy of children. Yet, when we expressed metabolic costs on a per stride basis at equivalent speeds, we found no difference

in the mass-specific cost per stride incurred by 5-7 year-old subjects in our shortest group vs. the 20-32 year-old subjects in the tallest group (Table 3). The absence of an age effect is similarly supported by the close agreement between the mass scaling exponents presented for human children plus adults with that established for adult vertebrates spanning a much greater body mass range (Taylor et al., 1981). A more recent, but less comprehensive, walking-specific vertebrate scaling value (Rubenson et al., 2007) similarly supports the conclusion that children walk at least as economically as adults when the effect of body size is taken into account. These observations suggest that humans establish mature walking patterns sometime before they reach six years of age.

Concluding Remarks

Although formulated for the basic purpose of relating stature and mass to the metabolic cost of human walking, the quantitative relationships we have identified have immediate potential application. Walking is the primary form of physical activity for the large proportion of the world's population and occurs in nearly all human habitats. Accordingly, dozens of predictive equations have been developed for use in clinical, military, recreational and other settings. By incorporating the fundamental effect of body size, the following expressions allow the metabolic energy expended during human walking to be estimated from a distance covered and either stature and mass combined, or mass alone:

$$E_{\text{trans}} / M_b = 3.80 \cdot L_b^{-0.95} \quad (\text{eq. 1})$$

$$E_{\text{trans}} / M_b = 7.98 \cdot M_b^{-0.29} \quad (\text{eq. 2})$$

where E_{trans} is given in Joules per meter, M_b is in kilograms and L_b is in meters. Because humans walk at or near the speeds that minimize the metabolic cost of walking the large majority of the time (Cavagna et al., 1983; Bornstein and Bornstein, 1976), these relationships allow the metabolic energy expended while walking on firm level surfaces to be estimated with a minimum of information.

Finally, we note that the new scaling relationships we introduce for the walking transport costs of humans also have general biological implication and application. In the former case, our finding that the transport costs of walking humans are substantially lower than the norms for terrestrial vertebrates (Taylor et al., 1981) by a virtually constant margin of one-third across the broad range of body masses examined here (Fig. 2B) can inform comparative and evolutionary arguments (Rubenson et al., 2007; Alexander, 2004; Carrier, 1984; Rodman and McHenry, 1980; Pontzer et al., 2009) that depend on quantitative estimates of the relative locomotor economy of humans. In the latter case, the new scaling relationships could provide more specific estimates of the locomotor costs of early hominids from fossil-based estimates of stature and mass.

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Figure Legends

Fig. 1. Mass-specific, gross metabolic rates (**A**), net metabolic transport costs (**B**) and the net metabolic transport costs to walk a forward distance equal to the body's stature (**C**) in relation to walking speed for groups differing in stature.

Fig. 2. Mass-specific net metabolic transport costs in relation to stature (**A**) and body mass (**B**) at the most economical walking speeds illustrated on logarithmic coordinates for the original data presented (open and closed circles and triangles) and qualifying literature values (open squares). Exponential relationships of best-fit are provided for the original data, and the original data plus literature data points. [Stature, original data: $E_{\text{trans}}/M_b = 3.41 \cdot L_b^{-0.90}$, $R^2 = 0.98$; original + lit. data: $E_{\text{trans}}/M_b = 3.80 \cdot L_b^{-0.95}$, $R^2 = 0.52$; Mass, original data: $E_{\text{trans}}/M_b = 7.98 \cdot M_b^{-0.31}$, $R^2 = 0.98$; original + lit. data: $E_{\text{trans}}/M_b = 7.98 \cdot M_b^{-0.29}$, $R^2 = 0.50$; Taylor et al, 1982: $E_{\text{trans}}/M_b = 10.71 \cdot M_b^{-0.32}$].

**Predicting metabolic rate across walking speed:
one fit for all body sizes?**

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Running head: Height, weight and speed predict walking energy expenditure

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Abstract

We formulated a “one-size-fits-all” model that predicts the energy requirements of level human walking from height, weight and walking speed. Our three-component model theorizes that the energy expended per $\text{kg}\cdot\text{stride}^{-1}$ is independent of stature at mechanically equivalent walking speeds. We measured steady-state rates of oxygen uptake of 78 subjects who spanned a nearly two-fold range of statures (1.07 to 2.11 m) and seven-fold range of body masses (16 to 112 kg) at treadmill speeds from 0.4 to $1.9 \text{ m}\cdot\text{s}^{-1}$. We tested the size-independence of the model by deriving best-fit equations in the form of the model on four stature groups ($n\geq 15$): short, moderately-short, moderately-tall, and tall. The mean walking metabolic rates predicted by these four independently derived equations for the same set of reference subjects ($n=16$; stature range: 1.30-1.90 m) agreed with one another to within an average of $5.2\pm 3.7\%$ at the four intermediate speeds in our protocol. We next evaluated the model’s gross predictive accuracy by dividing our 78 subjects into 39 stature-matched pairs of experimental and validation group subjects. The model best-fit equation derived on the experimental-group subjects predicted the walking metabolic rates of the validation-group subjects to within an average of $8.1\pm 6.7\%$ ($R^2=0.90$; $\text{SEE}=1.34 \text{ mls O}_2/\text{kg}^{-1}\cdot\text{min}^{-1}$). The predictive error of the ACSM equation ($18.0\pm 13.1\%$), which does not include stature as a predictor, was more than twice as large for the same subject group. We conclude that the energy cost of level human walking can be accurately predicted from height, weight and walking speed.

Introduction

The premise that the metabolic energy walking requires is set by gait mechanical demands is universally accepted. However, in more than a century of experimentation a broad predictive relationship that directly links the two has not come forth. The absence of a relationship has not resulted from any lack of scientific interest in the topic; hundreds of studies have investigated walking energetics for humans and other terrestrial species. Indeed, one could easily conclude from the exhaustive literature on human walking that the relationship is too complex to be described in simple quantitative terms (8, 23, 32, 42, 49).

However, the primary findings from the comparative work on terrestrial locomotion offer a more promising perspective (27, 31, 43, 47, 48, 58). These classical studies identified an economy of scale for locomotor energy expenditure and provided a mechanistic explanation for its basis. Early investigations (47) established that the energy expended to transport one kg of tissue one meter ($E_{\text{-trans}}, E \cdot \text{kg}^{-1} \cdot \text{m}^{-1}$) varied with the body mass (M_b) of the animal to the negative one-third power ($E_{\text{-trans}} \propto M_b^{-0.32}$). Subsequent experiments demonstrated that at the equivalent speeds of different-sized quadrupeds, such as trot-gallop transition speed, the mass-specific energy expended per stride was nearly invariant (27,45). In this latter case, the superior economy of the larger animals was explained by their greater limb and stride lengths. These results implied an inverse relationship between transport costs and leg lengths ($E_{\text{-trans}} \propto L_{\text{leg}}^{-1.0}$) at equivalent speeds.

Although a body-size dependency of human locomotor economy has been apparent since the middle of the last century (5), the experimental approaches developed by comparative

biologists have been applied only limitedly to humans. The few investigations of the body-size basis of human walking economy that have been undertaken have reported trends similar to those appearing in the comparative literature (21, 35, 54). The lone human analysis quantifying the scaling of walking transport costs with body mass at mechanically equivalent speeds (54) conformed closely ($E_{\text{trans}} \propto M_b^{-0.29}$) to the classic comparative results. This study also found that the mass-specific energy expended per stride at a single equivalent walking speed did not vary between small and large human walkers. Thus, at the single standardized speed examined, the walking transport costs of humans were inversely related to leg length ($E_{\text{trans}} \propto L_{\text{leg}}^{-0.95}$).

The apparent conformation of human locomotor mechanics and metabolic energetics to consistent patterns, and the overarching importance of walking energy expenditure for human health, function and physiological status, begs the question of why a mechanics-based relationship for predicting energy expenditure has not emerged. A primary reason appears to be a lack of integration between the experimental approaches thus far employed. Those studies focused on developing generalized equations for predictive purposes have typically relied more heavily on *post-hoc* statistical analyses than *a priori* mechanistic formulations (7, 16, 17, 37, 38, 52). Most have used regression analyses with limited incorporation of established knowledge or theory. For example, the Pandolf *et al.* (38) and ACSM (3) equations, which are the current predictive standards, were both derived empirically and without incorporating the influence of gait mechanics or limb lengths. In contrast, the more basic studies that have incorporated the germane physiological and mechanical relationships *a priori* have generally not been applied for predictive purposes (19, 21, 35, 54).

Our objective here was to develop a generalized predictive equation for human walking that draws on comparative traditions to more fully incorporate the influence of body size. For this purpose we formulated a simple, mechanistic, whole-body model of walking metabolism and gait mechanics that includes three basic variables: height, weight and walking speed. We acquired metabolic data across a broad range of level walking speeds for human subjects who spanned a two-fold range of statures and a seven-fold range of body masses to test two hypotheses. First, we hypothesized that the best-fit, empirical descriptions provided by our model would be similar when derived from short, moderately-short, moderately-tall and tall human walkers. Second, we hypothesized that our basic model would predict metabolic rates during level walking with appreciably greater accuracy than either of the two leading current standards, the ACSM and Pandolf *et al.* equations.

Methods

The Height-Weight-Speed Model

Our three component model of walking metabolism is illustrated in Fig. 1. Rates of energy expenditure are illustrated as a function of walking speed, with the former expressed in units of oxygen uptake per physiological convention. Mass-specific rates of oxygen uptake typical for a tall adult appear on the left Y-axis while metabolic rates, expressed in multiples of the body's resting rate (METs), appear on the right Y-axis. The standardized values, theorized to apply to an individual of any height and weight, have been included to illustrate the model's postulated applicability across a broad continuum of human body sizes. The model partitions gross walking metabolic rates into three components: 1) resting metabolism, 2) minimum walking metabolism, and 3) speed-dependent walking metabolism. The scientific rationale for the model follows.

Resting Metabolic Rate (RMR): The model's first component is the minimum metabolic rate needed to supply all the body's tissues at rest, or resting metabolic rate. This component, in contrast to the other two in the model, can be directly measured under standardized conditions. For modeling purposes, we have assumed that resting metabolic rates accurately represent the minimum metabolic rate needed to sustain the body's tissues at rest and during exercise, and that this quantity is constant across different walking speeds.

Minimum Walking Metabolic Rate (MWMR): The model's second component is the minimum metabolic rate needed, above the body's resting rate, for walking at any speed. We have termed this component the minimum walking metabolic rate. The primary contributors to the minimum walking metabolic rate are the metabolic costs incurred to maintain an upright posture and support the body's weight against gravity in a walking posture (10, 46). Secondary contributors include the slight elevations in cardiac and pulmonary muscle activity needed to support increased pulmonary oxygen uptake and cardiovascular transport (46), and perhaps other factors. For modeling purposes, we have assumed that the minimum walking metabolic rate, like resting metabolic rate, remains constant across walking speeds.

Speed-Dependent Walking Metabolic Rates (SDWMR): The model's third component is that portion of the gross walking metabolic rate attributable to walking speed. The primary contributor to this third model component is the increased metabolic cost of supporting the body's weight against gravity at faster walking speeds. This cost increases with speed as muscle fibers with greater rates of ATP utilization are recruited to support the body's weight during progressively shorter periods of foot-ground force application at faster speeds (28, 31, 40, 46). Secondary contributors include performing the limited mechanical work per step required to lift

and accelerate the body's mass, and the relatively small metabolic cost of swinging the limbs at faster walking speeds. Indirect evidence suggests that the two latter factors, although relatively small, do contribute to the increased slope of the metabolic rate-walking speed relationship across the fastest walking speeds (4, 14, 15, 18).

Formulaic Basis of the Model: Of the three basic predictors in the Height-Weight-Speed model, the most straightforward influence is that of the total weight supported against gravity, which is typically the weight of the body. This direct influence is present in experimental results from load carriage studies (9, 26, 38), longitudinal studies involving weight loss (6, 24, 29), cross-sectional studies comparing obese and non-obese individuals (14, 15, 33), mechanistic explanations of locomotor metabolism (10, 28, 31, 40, 45, 46), and in the form in which body mass has been widely incorporated into existing predictive equations (3, 16, 17, 19, 38, 51, 56, 57). All of the aforementioned experimental and predictive results are consistent with the conclusion that, when the other factors (height and walking speed) are held constant, a 1:1 relationship exists between the body weight supported and the metabolic energy walking requires. Hence, the widespread convention of expressing the metabolic rates observed during locomotion and other weight-bearing exercise in mass-specific terms enjoys extensive experimental support. Accordingly, we have incorporated body mass directly into all of the metabolic terms in our Height-Weight-Speed model as follows:

$$\text{VO}_{2\text{-gross}} = \underbrace{\text{VO}_{2\text{-rest}}}_{\text{Resting Metabolism}} + \underbrace{C_1 \cdot \text{VO}_{2\text{-rest}}}_{\text{Minimum Walking}} + \underbrace{(C_2 \cdot V^{\text{exp}}) \cdot \text{Ht}^{-1}}_{\text{Speed-Dependent}} \quad (1)$$

where $VO_{2\text{-gross}}$ is the body's total, or gross volume rate of oxygen uptake, $VO_{2\text{-rest}}$ is the body's resting rate of oxygen uptake, C_1 is a coefficient describing the minimum walking rate of oxygen uptake as a multiple of the resting rate, C_2 is the coefficient that describes speed-dependent increases in the rate of oxygen uptake as a function of the velocity of walking, V , raised to the exponent, exp , divided by the height, Ht , or stature of the individual. Hence, the sum of the model's second and third metabolic components represents the metabolic rate attributable to walking ($VO_{2\text{-walk}}$). To be consistent with prior literature, all the terms in Eq. 1 above are expressed in mass-specific units of oxygen uptake of $\text{mls } O_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$. Per our scientific objectives and both Fig. 1 and Eq. 1, the term metabolic rate is used to refer to mass-specific rates of oxygen uptake throughout the manuscript.

The quantitative form of the first of our model's three metabolic components ($VO_{2\text{-rest}}$, Eq. 1), the body's resting metabolic rate, is largely self-explanatory because resting metabolic rates are a standard and universally accepted measure. The second model component, the body's minimum walking metabolic rate, incurred predominantly by support and postural requirements, was assumed to be constant across speed at a fixed multiple of the body's resting metabolic rate ($C_1 \cdot VO_{2\text{-rest}}$, Eq. 1) largely on the basis of prior results (19, 21, 37, 54, 56). The most appropriate form for the model's third component, speed-dependent walking metabolic rate, is more difficult because the speed-induced increases in walking metabolic rates depend on stature (54). We postulated that the speed-dependent portion of walking metabolic rates would be an exponential function of velocity and an inverse function of height ($V^{\text{exp}} \cdot Ht^{-1}$) for the following reasons. First, both mechanics-based approaches and correlational modeling have been consistent in the finding that the increases in walking metabolic rates that occur with speed can

be reasonably well described as a function of the velocity of walking squared (19,38,51,56). Second, among individuals who differ in body size, metabolic rate increases that occur with increases in walking speed are systematically greater in shorter vs. taller individuals, and therefore inversely related to stature (21,54). Hence, the model's third metabolic rate term takes the form of a coefficient times walking velocity raised to an exponent divided by height $((C_2 \cdot V^{\text{exp}}) \cdot Ht^{-1}$, Eq. 1). In those instances in which *exp* has the theorized value of 2.0, this $V^2 \cdot Ht^{-1}$ term reduces to units of $m \cdot s^{-2}$.

Our model incorporates an existing solution for identifying speeds that are mechanically equivalent for individuals who differ in stature. This solution is derived from the principle of dynamic similarity, and has, in prior literature (1, 2, 54), taken the form of the Froude number: $U = V^2 \cdot (g \cdot L_{\text{leg}})^{-1}$ where U is equivalent speed, V is the velocity of walking, g is gravitational acceleration, and L_{leg} is leg length. Our prior result at a single equivalent speed indicated that different-sized human walkers do indeed walk in a dynamically similar manner (54), which by definition entails stride lengths, times and forces being related to the body's linear dimensions by a constant across the full continuum of body sizes (1,2). In addition, we found that the energy cost per $kg \cdot \text{stride}^{-1}$ for shorter and taller individuals at the one equivalent speed examined did not vary. If our prior metabolic result from one equivalent speed generalizes to other equivalent speeds, then a single term that includes the walking velocity squared divided by the linear dimensions of the body should accurately describe the speed-dependent metabolic rates of different individuals regardless of their height. Here, for simplicity and ease of use, we used a Froude number analogue that replaced leg length with body length (i.e. height) and dropped the gravitational acceleration term to become: $V^2 \cdot Ht^{-1}$.

Our equivalent speed term for this third model component led us to two specific predictions. First, speed-dependent increases in mass-specific metabolic rates should be linear when expressed in relation to the velocity of walking squared. Second, the differences in how rapidly metabolic rates increase as a function of speed for shorter vs. taller individuals should be an inverse function of both leg length and height. Neither gender nor age were included in the model because both mechanical theory and prior empirical results (54) indicate these variables do not influence walking economy independently of height, weight and speed in healthy individuals under 50 years of age.

Experimental Protocol and Measurements

Subjects: Two strategies were employed to maximize the range of body sizes and walking metabolic rates obtained. First, we recruited human subjects who spanned a wide range of heights and weights. Second, we tested subjects across a nearly 5-fold range of walking speeds from 0.4 to 1.9 m•s⁻¹. By recruiting children as young as five years of age and enrolling a number of individuals whose stature exceeded 2.0 meters (> 6' 6"), we obtained a nearly two-fold range of statures (1.07 to 2.11 m) and seven-fold range of body masses (15.9 to 112.8 kg) in our subject pool. We ultimately tested a total of 78 subjects, 45 males and 33 females, between the ages of 5 and 48 years. In accordance with local Institutional Review Board policies and procedures adults provided written informed consent while children provided written assent accompanied by the written consent of a parent or legal guardian. Subjects were healthy and generally free of obesity as only four of the 78 subjects had BMI values >30 kg•m⁻². Limited data from 48 of the 78 subjects were reported in a prior study (54). Height and weight were measured with a stadiometer and platform scale accurate to the nearest 0.001 m and 0.1 kg,

respectively. Leg lengths were measured by palpating the hip joint axis of rotation during standing and slow swinging of the limb in the sagittal plane.

Treadmill Testing Protocol: Subjects were asked to walk on a level treadmill at constant speeds of 0.4, 0.7, 1.0, 1.3, 1.6 and 1.9 m•s⁻¹. The protocol began with a 4- to 6-minute walking trial followed by six trials at the aforementioned speeds. Each trial lasted long enough to obtain a 2-minute, steady-state rate of oxygen uptake. Speeds were administered in a staggered fashion beginning at 0.7 m•s⁻¹. Subjects were given a 5- to 10-minute break after completion of the protocol before repeating all trial speeds a second time. Some of the shortest subjects did not complete trials at the fastest one or two protocol speeds because they could not do so without running.

Metabolic Measures: A computerized metabolic system (Parvo Medics TrueOne 2400, Sandy, Utah) was used to measure rates of metabolic energy expenditure as assessed from measured rates of oxygen uptake (11). Samples of expired gases during steady-state treadmill walking were taken and analyzed for CO₂ and O₂ fractions using infrared and paramagnetic gas analyzers, respectively. Respiratory gases were collected using a one-way breathing valve that directed expired air through a pneumotach into a mixing chamber before analysis. For each speed, rates of oxygen uptake were averaged over a two-minute, steady-state period and the steady-state values from the two protocol repetitions were averaged for subsequent data analysis (54). Calibration was performed using a three-liter syringe to direct air through the system at volume flow rates similar to ventilation rates encountered during testing. A two-point calibration procedure was used to calibrate the gas analyzers using room air and a gas cylinder containing known concentrations of O₂ and CO₂ in the physiological range for expired gases. The TrueOne

system was also validated in the range of rates of oxygen uptake from 0.3 to 1.01 liters•min⁻¹ via simulations using precision blended N₂–CO₂ mixtures according to the infusion technique described by Moon *et al.* (36). The agreement between the rates of oxygen uptake measured by the TrueOne system across 15 infusion tests spanning these simulated rates of oxygen uptake was < 3.0% as previously reported (54).

In previous work, we have converted measurements of oxygen uptake to metabolic rates or rates of energy expenditure using an energetic equivalent of oxygen of 20.1 Joules per ml of O₂ (11). However, given the largely applied objective of the present study and existing literature conventions, here we report all results as rates of oxygen uptake (mls O₂•kg⁻¹•min⁻¹) without conversion to true units of energy for ease of interpretation.

Kinematic Measures: Walking kinematics were obtained using a 30 Hz video (Sony model DCR-TRV19, 30Hz). Stride times (t_{str}) were determined by counting the frames of twenty-five sequential contact periods of the same foot. Stride time was defined as the time between successive footfalls of the same foot. Stride frequency, the inverse of stride time, was determined in order to quantify the energy expended per kg•stride as previously (54, where $E \cdot \text{kg}^{-1} \cdot \text{stride}^{-1} = \text{VO}_{2\text{-walk}} \cdot t_{\text{str}}^{-1}$).

Data Treatment, Analysis and Hypothesis Tests

Data Management: Two considerations guided our model from scientific formulation to hypothesis testing: predictive accuracy and ease of use. We maximized predictive accuracy by allowing three numerical values in our model to be those that provided the best fit to the data across the broad ranges of height, weight, walking speeds and metabolic rates in our data set. These three values were: the coefficient describing the minimum walking metabolic rates (C_1),

the coefficient describing speed-dependent increases in metabolic rates (C_2), and the exponent (exp) describing speed-dependent increases in metabolic rates (Eq. 1). The optimization function in Excel (25; Microsoft Excel Solver, Excel 2010 version) was used for this purpose because this tool has the ability to identify the three aforementioned values whilst other model inputs (height, weight, estimated RMR, and walking velocity) were fixed at their known values. Thus, the values of C_1 , C_2 and exp that we report were those that allowed our model to best fit (i.e. maximized the explained variance) the experimental group metabolic rate data using a linear model. We used estimated rather than measured resting metabolic rates (VO_{2-rest}) because the majority of potential users do not know, and cannot acquire their measured resting values. The equations of Schofield *et al.* that we used for this purpose (44) have been extensively validated and are typically accurate to within $0.5 \text{ mls O}_2 \text{ kg}^{-1} \cdot \text{min}^{-1}$ or less (22, 30, 39, 41, 50, 55). Hence, any error introduced by using estimated, rather than directly measured RMR values, is likely to constitute a very small fraction of gross metabolic rates during walking in accordance with our prior findings (54).

Hypothesis Test One: We tested our first hypothesis that the best-fit, empirical descriptions provided by our model would not differ for human walkers of different statures in the following manner. We divided our sample of 78 total subjects into four groups exclusively on the basis of height to obtain: a short group (A), moderately-short group (B), moderately-tall group (C) and a tall group (D). We then extracted four subjects from the mid-range of statures within each of these groups to form a reference group with subjects who, with respect to stature, were representative of each of the four groups from which they were drawn. Four fully independent best-fit metabolic rate-speed equations were then derived in the form of the Height-Weight-

Speed model (Eq. 1) using the walking metabolic rate data obtained from the subjects in each of the four respective stature groups. This process produced four best-fit equations with values of C_1 , C_2 and exp derived independently and to optimize the model fit to subjects of different statures. The number and characteristics of the subjects from the four stature and one reference group appear in Table 1.

Once derived, the respective equations from each of the four stature groups were then used to generate predicted walking metabolic rate values at each of the six walking speeds in our protocol. Our expectation was that due to the manner in which our model incorporates height, weight and walking speed, that the values predicted at each speed would be similar despite being derived on groups that differed in stature and body mass. The subject-specific model inputs required to generate the predictions: height, weight and estimated RMR, were in each case provided by the reference group subjects to hold the input variables fully constant across the four predictive equations. We specifically evaluated whether the metabolic rate predictions generated by the four stature group equations differed significantly by using a two-way ANOVA ($\alpha < 0.05$) that tested for the main effects of stature group and walking speed.

Hypothesis Test Two: We tested our second hypothesis that our basic model would, after empirical refinement, predict walking metabolic rates during level walking appreciably more accurately than either the ACSM or Pandolf *et al.* equations as follows. We split our sample total of 78 subjects into experimental and validation groups of 39 subjects each. One subject from each of 39 pairs of stature-matched individuals was randomly assigned to the experimental group while the remaining member of the pair was assigned to the validation group. The heights, weights and genders of the experimental and validation group for hypothesis test two also appear

in Table 1. A best-fit equation in the form of Eq. 1 was developed from the measured metabolic rates of the experimental group subjects. As with hypothesis test one, the coefficients C_1 and C_2 and exponent exp were allowed to vary in order to provide the best linear fit to the metabolic rate data of the experimental group. The best-fit equation derived on the experimental group was then used to predict the walking metabolic rates measured for the subjects in the validation group subjects at each of the six walking speeds. The overall agreement between measured values and those predicted by the model was assessed from the proportion of total variance in walking metabolic rates accounted for (R^2) via linear regression and deviation from the line of identity. The accuracy of the individual predictions was assessed using the standard error of estimate (SEE). We hypothesized that the predictive error of the Height-Weight-Speed model would be less than half that of the ACSM and Pandolf *et al.* equations for the group of subjects and speeds tested here.

In addition to the ACSM and Pandolf equations, and to provide a more comprehensive perspective on the relative predictive accuracy of our Height-Weight-Speed model, we also generated predictions from three other prominent predictive equations in the literature: Cotes & Meade (19), van der Walt & Wyndham (51), and Workman & Armstrong (56).

Results

Part I - Representative Subject Data to Illustrate the Height-Weight-Speed Model

Metabolic Rates – Gross, Net Walking, and Speed-Dependent Rates vs. Absolute Speed: The gross metabolic rates of four representative subjects whose heights (A-1.15, B-1.47, C-1.78, and D-2.06 m) spanned a 1.8-fold range appear in Fig. 2. The taller the individual, the lower the gross metabolic rates were at any given speed (Fig. 2A). Similarly, speed-induced increases in these rates also tended to be smaller for taller subjects. Differences between the shortest and tallest individuals in gross metabolic rates were in approximate proportion to their stature difference, being roughly two-fold at each of the common speeds completed. A portion of the difference in gross rates was attributable to the greater RMR values estimated for the shorter individuals (Fig. 2D). When the first two metabolic components of the model, estimated RMR and MWMR (Fig. 1, Eq. 1), were sequentially subtracted to provide net walking metabolic rates (gross – RMR), and subsequently speed-dependent walking metabolic rates (gross – [RMR + MWMR]), the patterns observed for gross rates remained largely intact, but were substantially reduced (Fig. 2G). For each of the three expressions of walking metabolism, and each of the four individuals, metabolic rates increased in a curvilinear fashion with walking speed.

Metabolic Rates vs. Equivalent Walking Speeds: For the three expressions of walking metabolism, and each of the four individuals, metabolic rates increased in a curvilinear fashion with walking speed and per above, these increases tended to be smaller for the taller individuals (Fig. 2A, D, G). When increases were plotted in relation to speed of walking squared, a slight curvilinear trend remained for each of the three metabolic expressions and for all four

individuals, as did small individual differences in the rates at which metabolic rates increased (Fig. 2B, E, H). However, when the metabolic rate vs. speed² relationship was subsequently divided by the stature of the individual, the small differences present prior to this stature standardization were essentially fully eliminated for all three of the metabolic expressions illustrated (Fig. 2 C, F, I). Finally, when both RMR and MWMR were subtracted from gross metabolic rates, the slopes of the SDWMR of the four different individuals became essentially the same (Fig. 2I).

Part II - Energy Expenditure per Stride at Equivalent Walking Speeds

The mass-specific metabolic costs per stride at our index equivalent speed of $V^2 \cdot Ht^{-1}$ for the four stature groups formed for hypothesis test one appear in Fig. 3. Per stride costs were relatively constant across slower standardized speeds at values of approximately $0.12 \text{ mls O}_2 \cdot \text{kg}^{-1} \cdot \text{stride}^{-1}$ before increasing at the faster standardized, or equivalent, walking speeds to maximum values that were twice those observed at slower speeds ($0.24 \text{ mls O}_2 \cdot \text{kg}^{-1} \cdot \text{stride}^{-1}$). The patterns across speed and values at slow, moderate and faster equivalent speeds were similar across all four stature groups. However, a trend for the taller subjects to be slightly less economical at all of the standardized speeds was present.

Part III – Hypothesis Test Outcomes

Hypothesis Test One: One Fit from Different Body Sizes? The gross metabolic rates predicted by the four independent best-fit equations derived from the four stature groups formulated to test hypothesis one appear in Fig. 4. The derived values for the coefficients C_1 , C_2 and exp for each of the four groups that were used to generate the predictions illustrated appear in Table 2 accompanied by the R^2 and SEE values for each of the respective within-group fits. The

metabolic rates predicted using the four equations increased with speed (ANOVA, $p < 0.001$) from mean values at the slowest speed of $0.4 \text{ m}\cdot\text{s}^{-1}$ of $7.5 \pm 0.3 \text{ mls O}_2\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$ to values of $19.0 \pm 0.5 \text{ mls O}_2\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$ at $1.9 \text{ m}\cdot\text{s}^{-1}$. In addition to similar values being predicted at the different protocol speeds, the overall pattern of increase for the metabolic rate-speed relationship was also similar across the four groups. The main effect of stature group on predicted metabolic rates was not significant (ANOVA, $p = 0.13$). The mean values predicted by the four equations for the reference group subjects agreed with one another to within an average of $5.2 \pm 3.7\%$ across the four intermediate speeds in the protocol ($n = 16$ comparisons).

Hypothesis Test Two: A More Accurate Generalized Equation? The relationship between the metabolic rates predicted by the ACSM and Pandolf *et al.* models and the metabolic rates measured for the 39 subjects in our validation group appear in Fig. 5A and B. The proportion of the total variance of the walking metabolic rates measured for these subjects as provided by the R^2 value vs. the line of identity was 0.35 and 0.40 for the ACSM and Pandolf *et al.* equations, respectively, with corresponding SEE values of 3.35 and $3.23 \text{ mls O}_2\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$, respectively. For the Height-Weight-Speed model derived here, the corresponding R^2 value for the proportion of the total variance accounted for was 0.90, while the SEE for the predicted values was $1.34 \text{ mls O}_2\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$ (Fig. 5C). Hence, the error of individual prediction was roughly 2.5 times greater for ACSM and Pandolf *et al.* vs. the Height-Weight-Speed model. The relatively poorer predictive accuracy of the ACSM and Pandolf *et al.* equations resulted primarily from substantial under-predictions of the greater gross metabolic rates of the shorter subjects.

In addition to the generalized equation derived from the experimental group formed to test hypothesis two that appears in Table 2, we also derived a simplified version of the equation

with C_1 fixed at 1.00 and the exponent fixed at 2.00. The accuracy of the predictions provided by this simpler form of the equation differed little from the original equation reported in Table 2 ($R^2=0.87$; $SEE=1.53 \text{ mls O}_2\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$).

The predictive accuracy of our Height-Weight-Speed model was essentially unchanged when leg length (L_{leg}) was used as a model predictor instead of height. In this case, the best-fit equation derived on the experimental group using leg length rather than height in the model ($\text{VO}_{2\text{-gross}} = \text{VO}_{2\text{-rest}} + 0.097 \cdot \text{VO}_{2\text{-rest}} + (2.56 \cdot V^{2.38}) \cdot L_{\text{leg}}^{-1}$) accounted for a slightly smaller proportion of the total variance with a slightly greater standard error of estimate ($R^2=0.87$; $SEE=1.49 \text{ mls O}_2\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$) when predicting the walking metabolic rates of the validation-group subjects.

Discussion

Basic and applied motivations led us to formulate and test a simple, whole-body model that predicts the energy cost of level human walking from height, weight and walking speed. The model is consistent with the body-size trends previously reported for human locomotor economy and physical principles that apply to the gait mechanics of terrestrial species from rodents to dinosaurs (1, 2). In keeping with our first hypothesis, the empirical, best-fit equations in the form of the model independently derived from four groups of subjects who differed in both stature and mass (Table 2) provided similar predictions. The mean values predicted from these four distinct model-derived equations for the same set of reference subjects agreed with one another to within an average of $5.2 \pm 3.7\%$ for the four intermediate speeds in our protocol (Fig. 4A) that encompass the range of speeds humans typically self-select in the field (13, 18). As hypothesized for our applied second hypothesis, the best-fit model equation derived on half of our subjects predicted the walking metabolic rates of the stature-matched remaining half to within $8.1 \pm 6.7\%$ on average ($R^2 = 0.90$; $SEE = 1.34 \text{ mls O}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$), and appreciably more accurately than existing literature alternatives. Given the nearly two-fold range of statures and seven-fold range of body masses of the subjects tested, these results indicate that the answer to the “one fit for all sizes” question posed in our title is largely positive. Consequently, we conclude that the energy cost of human walking on firm, level surfaces can be accurately predicted from three basic variables: height, weight and walking speed.

Mechanistic Basis of the Height-Weight-Speed Model

From the outset, we postulated that a direct link between walking gait mechanics and metabolism would explain the stature-related trends long observed for human walking economy. We expected the greater metabolic rates of shorter vs. taller individuals at any given speed, and the greater increases across speed (Fig. 2A, D, G) to be fully explained by greater stride frequencies with no appreciable differences in per stride metabolic costs ($\text{mls O}_2 \cdot \text{kg}^{-1} \cdot \text{stride}^{-1}$). In our model, these expectations translated into per stride metabolic costs that were theorized to be invariant for subjects of different statures walking at mechanically equivalent speeds. Did these theoretical expectations match the empirical results obtained?

The walking metabolic rates of the four stature groups formed to test hypothesis one, when divided by respective stride rates to obtain per stride costs, were indeed similar when expressed in relation to our index of equivalent speed ($V^2 \cdot Ht^{-1}$, Fig. 3). Both the mean values for the energy expended per $\text{kg} \cdot \text{stride}^{-1}$ and the sigmoidal patterns of increase across equivalent speeds for the four different stature groups were largely the same, albeit with a consistent trend for the tallest stature group to have marginally greater values than the other three. These results support the basic mechanistic premise of our model that the mass-specific metabolic energy expended to execute each component of the walking stride should be the same at mechanically equivalent speeds for individuals who differ in stature. The coupling observed between gait mechanics and metabolic rates across body sizes at equivalent walking speeds provides two basic conclusions. First, the size-based trends long noted for human locomotor economy across walking speeds and previously considered largely (37, 52, 53) or partially (21, 35) in terms of age are attributable to a common link between body size and gait mechanics. Second, the mass-specific locomotor economy of humans, like that of non-human terrestrial species (27, 45, 46),

has a per stride mechanistic basis that becomes evident when comparisons are at mechanically equivalent speeds.

While per-stride metabolic costs can be readily assessed, the mechanistic validity of the three metabolic components of our model (Fig. 1), for reasons both general and specific, is more difficult to evaluate. From a general standpoint, models as parsimonious as the one offered here inevitably simplify biological reality to some degree. From a specific standpoint, evaluating the mechanistic validity of our model's metabolic components was not an objective that directly aligned with our primary goal of assessing the model's gross predictive accuracy. These limitations withstanding, the contributions of the three metabolic components of the model, and their inferred contributions as a function of absolute and relative walking speeds did correspond well to theoretical expectation. This is best illustrated by the representative data presented in Fig. 2 in which successive metabolic components were removed to illustrate gross, net walking and speed-dependent walking metabolic rates, respectively, for four individuals who differed in stature. These results support the model's general validity, and suggest the model may have value as an experimental tool for advancing basic understanding. In this latter regard, the parsimony and defined metabolic components of the model should serve as an experimental asset rather than a liability. In contrast to the many empirically-derived predictive equations formulated with limited deterministic basis (3, 7, 16, 17, 37, 38, 52), each of the terms in our Height-Weight-Speed model has been defined, and therefore represents a potentially testable biological entity.

Hypothesis Test One: Body-Size Independence

As expected for hypothesis test one, the metabolic rates predicted for the same group of subjects from model equations derived independently on groups of short, moderately-short, moderately-tall, and tall subjects differed little in magnitude and not at all statistically. When assessed at the intermediate speeds in our protocol that encompass the speed range humans typically self-select (13, 18, 34), we found the average agreement between the mean values predicted by the four respective equations for the same group of reference subjects was just over 5.0% (Fig. 4A). This led us to conclude that the stature of the subjects on whom the model equation was derived had little effect on the predictions provided. In addition to the predicted means agreeing closely with one another, they also were in good agreement with the values actually measured for the reference subjects at these intermediate speeds, with the average agreement between the means predicted by the four respective equations and those measured being $3.9 \pm 3.7\%$. In contrast, the predictions from five of the leading equations from the literature for the same four speeds ($n=20$ comparisons) differed from each other by an average of $13.8 \pm 8.4\%$ and from the measured values by $9.5 \pm 7.5\%$ (Fig. 4B).

Although our primary test of an effect of body size on the model predictions provided was negative, there was a consistent trend for the tallest subjects to be slightly less economical than strictly theorized. This trend was first apparent in the gross metabolic rate predictions generated by the equation derived on the tallest subjects. These values tended to be slightly greater than those predicted from the equations derived on the three shorter groups, particularly at the slowest walking speeds (Fig. 4A). Mathematically, these small predictive differences resulted from best-fit values for the coefficient C_1 , which describes the increase above RMR constituted by the minimum walking metabolic rate, being greatest for the tallest group (Table 2).

Indeed, across the four groups, the C_1 values derived increased slightly, but consistently, with the mean stature of the group. Because these C_1 differences were small, the resulting differences in metabolic rates predicted were also small, with little effect being discernible in the predictions provided from the equations derived on the shortest three groups. However, in the case of the tallest group, the metabolic rates predicted were slightly, but consistently greater across walking speeds. While one possible explanation for the limited variation observed in the group C_1 values derived is modeling artifact, empirical observations indicate otherwise. Specifically, the slightly poorer per-stride economy directly measured for the tallest subject group vs. the other three stature groups across equivalent walking speeds (Fig. 3) indicates that a small, but measurable biological difference is present. Thus, as reflected in the greater C_1 values derived for the tallest group, our results suggest that human walking economy has a slight stature dependency even after gait mechanics have been accounted for. For reasons not yet clear, tall individuals walk slightly less economically in terms of mass-specific per-stride metabolic costs and related gait mechanics that are incorporated into our model.

Hypothesis Test Two: Predictive Accuracy

Fair consideration of the relative predictive accuracy of the two leading literature equations evaluated here warrants the acknowledgment of two factors. First, in contrast to the new model introduced here, the ACSM and Pandolf *et al.* equations were formulated on, and meant to be applied to, adult-only subject populations. Second, both ACSM and Pandolf *et al.* are generalized equations that incorporate the influence of factors not presently included in the Height-Weight-Speed model. Specifically, the ACSM equation quantifies the influence of

surface inclination in addition to body mass and speed (3). The Pandolf *et al.* equation quantifies the influence of surface inclination, load carriage, speed and terrain (38). Hence, these two leading literature standards were developed for, and have, a greater breadth of application than our Height-Weight-Speed model does at present.

However, a primary motivation for formulating our new model was the recognition that existing predictive models do not include what appears to be one of the three basic determinants of human walking economy: stature. The potential consequences of omitting stature from predictive equations include poorer predictive accuracy and systematic error. These consequences would likely be most evident in the predictions provided for a stature-stratified group of subjects such as that tested here. However, given the basic influence of stature on gait mechanics and accompanying patterns of locomotor metabolism, predictive accuracy is likely to be compromised among more stature-homogeneous subjects also, but simply to a lesser degree. Both of these expectations were borne out in our results. First, in the original stature-stratified validation group of 39 subjects, the average error of prediction from our Height-Weight-Speed model was less than half that of the ACSM and Pandolf *et al.* equations as hypothesized, being $8.1 \pm 6.7\%$ for our model vs. 18.0 ± 13.1 and $21.0 \pm 14.4\%$ for ACSM (3) and Pandolf *et al.*, (38) respectively. The greater predictive error in these two established literature equations resulted primarily from consistent under-predictions of the metabolic rates of the shorter subjects in our sample (Fig. 5A and B). However, when we narrowed the range of statures to include only subjects in the typically adult range of 1.50 to 1.90 meters, a roughly two-fold difference in predictive accuracy remained. In the latter case, for the 28 subjects in the validation group within this range of typical adult statures, the average error of the individual predictions for the Height-

Weight-Speed model was $8.4 \pm 7.2\%$ vs. $15.2 \pm 10.7\%$ and $17.5 \pm 12.5\%$ for ACSM and Pandolf *et al.*, respectively.

Next, we examined the individual-case consequences of including stature, or not, in predictive equations using the walking metabolic rate data acquired from three individual subjects in our data set: one short, one of average-height, and one tall (Fig. 6A, B, and C, respectively). Also appearing in the three-paneled illustration are the predictions provided for each individual by five, well-established literature equations that appear in Table 4: ACSM (3), Pandolf *et al.* (38), Cotes & Meade (19), van der Walt & Wyndham (51), and Workman & Armstrong (56), as well as the Height-Weight-Speed model introduced here. The first four of the aforementioned predictive equations do not include stature as a predictor, and thus provide identical predictions of the mass-specific metabolic rates for each of the three individuals at each of the speeds illustrated. In contrast, the metabolic rates actually measured for these individuals at common speeds vary over a roughly two-fold range, and do so in inverse relation to their statures. Thus, the consequence of not including stature as a predictor is significant under-estimations for the short individual and significant over-estimations for the tall individual by all four of the predictive equations that do not include stature.

The accuracy of the two remaining equations illustrated, Workman & Armstrong (56) and the Height-Weight-Speed model, is appreciably better for the three individuals illustrated because these equations do include stature as a predictor. The predictions provided across speed for each of the three individuals by these two equations vary inversely, to some degree, with stature, and therefore in greater accordance with the walking metabolic rates measured. The stature-related variability present is predicted less accurately by the Workman & Armstrong equation, despite its

appreciably greater complexity (Table 4), because the quantitative influence of stature was probably not fully discerned during the development of this model. One noteworthy comparison between these latter two equations is that our Height-Weight-Speed model captures a larger proportion of the stature-related variation with an equation that has fewer than half as many terms.

Concluding Remarks

The primary goal of our basic approach to integrating body size, gait mechanics and locomotor metabolism was to provide a translational advance in the form of an improved generalized equation for predicting the energy requirements of human walking on firm, level surfaces. Although gait mechanics and physiological function during walking are complex, our basic approach led to an equation with one speed-dependent term and two constants to explain the variation in walking metabolism introduced by both body size and walking speed. In closing, we put forth several suggestions for easy utilization of the translational tool offered. First, we recommend using the gender, age and mass-based RMR estimates provided by the Schofield *et al.* equations in Table 3 given their well-established accuracy and the impracticality of obtaining direct RMR measurements in most circumstances. Second, because the second metabolic term in the model is a multiple of the first, the two can be combined into a single term. Since the model value empirically identified for the second metabolic term was generally equal to the first (Table 2, see C_1 values ≈ 1.0), this combined term can be well described as the RMR multiplied by two. Third, although the model exponent that originally provided the best fit to our experimental group data was 2.34, the predictive improvement offered vs. the theorized exponential value of

2.00 was negligible. In combination, these observations lead us to offer the following simplified equation for general predictive purposes:

$$\text{VO}_{2\text{-gross}} = 2.0 \cdot \text{VO}_{2\text{-rest}} + 5.6 \cdot V^{2.0} \cdot \text{Ht}^{-1} \quad (2)$$

where $\text{VO}_{2\text{-gross}}$ and $\text{VO}_{2\text{-rest}}$ (44, Table 3) are expressed in $\text{mls O}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$, V is in $\text{m} \cdot \text{s}^{-1}$ and Ht is in meters. The accuracy of prediction using the simplified expression of the model in Eq. 2 differs negligibly from the original. The increase in the SEE of the prediction increased by < 0.2 $\text{mls O}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$ when using the simplified vs. originally-derived equation to predict the metabolic rates of the validation group subjects.

Clearly, additional experimental work is required to determine how well the Height-Weight-Speed model might describe walking metabolism under conditions not tested here, such as graded surfaces, load carriage and variable terrain. Nonetheless, by including the influence of stature on gait mechanics and walking metabolism as we have, our new model provides accurate predictions of the energy requirements of level walking, and does so from a concise equation with discrete, testable components.

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Figure Captions

Fig. 1. A schematic illustration of metabolic rate vs. speed that partitions the body's total or gross metabolic rate into the three contributing components postulated by the Height-Weight-Speed model: resting metabolic rate, minimum walking metabolic rate and speed-dependent walking metabolic rate. Metabolic rates are provided in units of oxygen uptake rates (left-hand Y-axis) and multiples of the body's resting metabolic rate (METs, right-hand Y-axis). The rates of oxygen uptake plotted correspond to those of a relatively tall, non-obese adult while those plotted as multiples of the body's resting metabolic rate are theorized to apply to non-obese individuals across a broad continuum of heights and weights.

Fig. 2. The walking metabolic rate-walking speed relationship of four individual subjects (A, B, C, D) who differ in stature, expressed in terms of the metabolic components (rows) and equivalent speed standardization of the Height-Weight-Speed model (columns). Panels in the descending rows illustrate three metabolic rate variables: gross metabolic rates (A, B, C), gross – resting metabolic rates (D, E, F), and gross – (resting + minimum walking) metabolic rates (G, H, I), each plotted vs. three expressions of walking speed: absolute walking speed (left column panels), walking speed squared (middle column panels) and walking speed squared•height⁻¹ (right column panels). [Curves in the left and middle columns were fit with second-order polynomials while those in the right-hand column were fit with linear functions].

Fig. 3. The mass-specific energy expended per walking stride for the four different stature groups expressed as a function of equivalent walking speed. Per stride energy expenditure at any

equivalent speed and across equivalent speeds was similar for short, moderately-short, moderately-tall and tall groups

Fig. 4. The gross walking metabolic rates vs. speed predicted for the same groups of reference subjects by each of the four Height-Weight-Speed model equations derived on the four different stature groups (A). The gross metabolic rates predicted for the reference group subjects by five well-established predictive equations from the literature (B). The metabolic rate means measured for the reference group subjects at each speed appear in both panels for comparison.

Fig. 5. The gross walking metabolic rates measured for the validation-group subjects vs. those predicted by the ACSM equation (A), the Pandolf *et al.* equation (B) and the Height-Weight-Speed model (C). The error of the individual predictions (SEE) of both the ACSM and Pandolf *et al.* equations was two to three times greater than that of the Height-Weight-Speed model.

Fig. 6. Gross walking metabolic rates for a short (A), average height (B) and tall subject (C) across walking speeds vs. the rates predicted by the leading literature equations and the Height-Weight-Speed model introduced here. Because four of the five leading literature equations do not incorporate stature as a predictor, these equations systematically under-predict the walking metabolic rates of short individuals and over-predict the metabolic rates of tall ones. In contrast, the Height-Weight-Speed model accurately accounts for most of the metabolic rate variation introduced by the stature of the subject.

Tables

Table 1. Physical characteristics of the subgroups for hypotheses 1 and 2

Hypothesis 1	n (male)	Age (years)	M _b (kg)	L _b (m)
Stature Groups				
1	15 (6)	8.3 ± 0.8	32.9 ± 4.1	1.30 ± 0.04
2	15 (5)	17.3 ± 2.3	58.0 ± 3.4	1.58 ± 0.01
3	16 (9)	20.8 ± 1.3	65.5 ± 2.4	1.70 ± 0.01
4	16 (15)	21.8 ± 0.9	87.6 ± 3.2	1.90 ± 0.03
Reference Group	16 (10)	19.6 ± 2.9	63.5 ± 4.8	1.62 ± 0.05
Hypothesis 2				
Experimental Group	39 (23)	17.5 ± 1.5	63.0 ± 3.6	1.63 ± 0.04
Validation Group	39 (22)	17.9 ± 1.3	60.8 ± 3.6	1.62 ± 0.04

Values are means ± SE

Table 2. Empirical derivations of model components

Hypothesis 1	n	C ₁	C ₂	Exponent	R ²	SEE
Stature Groups						
1	15	0.87	4.37	2.74	0.90	1.30
2	15	0.98	4.73	2.31	0.92	1.16
3	16	1.10	3.71	2.67	0.92	1.24
4	16	1.29	3.83	2.57	0.90	1.20
Hypothesis 2						
Experimental Group	39	0.97	4.87	2.34	0.89	1.45

Stature, meters

SEE, ml·kg⁻¹·min⁻¹

Table 3. Schofield et al. equations for predicting RMR from gender, age and body mass

Age (years)	Male	Female
Under 3	$\text{RMR} = 8.603 - (4.388 * \text{wt}^{-1})$	$\text{RMR} = 8.43 - (4.491 * \text{wt}^{-1})$
3-10	$\text{RMR} = 3.282 + (72.899 * \text{wt}^{-1})$	$\text{RMR} = 2.937 + (70.239 * \text{wt}^{-1})$
10-18	$\text{RMR} = 2.557 + (95.149 * \text{wt}^{-1})$	$\text{RMR} = 1.935 + (100.124 * \text{wt}^{-1})$
18-30	$\text{RMR} = 2.177 + (100.055 * \text{wt}^{-1})$	$\text{RMR} = 2.142 + (70.343 * \text{wt}^{-1})$
30-60	$\text{RMR} = 1.658 + (126.209 * \text{wt}^{-1})$	$\text{RMR} = 1.175 + (122.236 * \text{wt}^{-1})$
Over 60	$\text{RMR} = 1.693 + (84.957 * \text{wt}^{-1})$	$\text{RMR} = 1.313 + (95.184 * \text{wt}^{-1})$

RMR, resting metabolic rate

wt, body weight in kilograms

RMR is in VO_2 units ($\text{ml} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$)

Table 4. Prediction equations from prior literature

Equation	Reference
$VO_2 \text{ (ml} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}) = (0.1 \cdot V) + (1.8 \cdot V \cdot G) + 3.5 \text{ ml} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$	ACSM, 2006
$VO_2\text{-equiv (watts)} = 1.5 \cdot M + 2.0 \cdot (M + L)(L/M)^2 + \eta(M + L)[1.5 \cdot V^2 + 0.35 \cdot V \cdot G]$	Pandolf <i>et al.</i> , 1977
$VO_2 \text{ (L} \cdot \text{min}^{-1}) = 0.00800 \cdot M + 0.000245 \cdot M \cdot V^2$	Cotes & Meade, 1960
$VO_2 \text{ (L} \cdot \text{min}^{-1}) = 0.00599 \cdot M + 0.000245 \cdot M \cdot V^2$	van der Walt & Wyndham, 1973
$VO_2 \text{ (L} \cdot \text{min}^{-1}) = Ht \cdot (0.0136 \cdot Ht - 0.375)^{-1} \cdot (1.92 \cdot V^{0.176} - 1.445) \cdot M \cdot (0.82 \cdot V^2 - 3.94 \cdot V + 9.66) \cdot 10^{-5}$	Workman & Armstrong, 1963

V – velocity*, M - body mass**, Ht – height (inches), L – load (body mass units), G - grade (%), η - terrain factor, (arbitrary units).

*Units for velocity are reference-specific as follows: V, velocity; ACSM: meters per minute ($\text{m} \cdot \text{min}^{-1}$); Pandolf et al: meters per second ($\text{m} \cdot \text{s}^{-1}$); Coates & Meade: meters per minute ($\text{m} \cdot \text{min}^{-1}$); van der Walt & Wyndham: kilometers per hour ($\text{km} \cdot \text{hr}^{-1}$); Workman & Armstrong: miles per hour ($\text{mi} \cdot \text{hr}^{-1}$).

**Units for M are in kg for all the above equations except for Workman & Armstrong which uses body weight in pounds (lb).